

THE SOUTH HAVEN PENINSULA SURVEY (STUDLAND HEATH, DORSET): GENERAL SCHEME OF THE SURVEY¹

By C. DIVER AND R. D'O. GOOD.

IN 1931 an attempt was made to map in detail the distributions of the grass-hopper species found within a defined part of Studland Heath (Diver, C. and P., 1933). This preliminary trial showed that the much more ambitious scheme of a *complete* biological study of the peninsula was, at the least, worth attempting; and work was at once begun both upon the history of the area and upon such surveys of plant and animal groups as could then be undertaken. The area to be surveyed was increased so as to include all of the peninsula that falls within easily defined boundaries, and as now delimited contains roughly 750 acres of which about 80 are under inland water (Diver, 1933). An examination of the flowering plants and ferns has been made and a general account of their ecology has been completed (Good, in press); a second paper including geographical and floristic analyses of the vegetation and its comparison with that of similar areas elsewhere is in preparation. With the essential framework of the plant distribution determined, it is our object to bring into action a body of workers who, while making separate studies of the groups in which they are specialists, will yet do so with a co-ordination in attack and a unity in aim towards the ultimate objective—the elucidation of the complex bonds that hold together a complete society of plants and animals.

The peninsula has great biological importance and this is largely due to its remarkable history. Since it is a coastal strip at the mouth of a harbour its topography has been well surveyed in the past. Thus a reasonably clear history of the physiographical and other changes that have taken place in the last 300 years can be constructed (Diver, 1933). Though it is a classic locality long known to biologists, no previous co-ordinated effort appears to have been made to examine the area in any detail or to follow the very rapid changes that have taken place even during the present century; much valuable information has, therefore, already been lost. However, changes are even now in progress and the area is still one peculiarly suited to the study of the responses made by populations to an unstable environment.

A detailed map, on a scale of 6 in. to the mile, has been published and, through the courtesy of the Director-General of the Ordnance Survey, this bears the new national grid drawn in 100 yard squares. The value of such a grid in work of this kind is too obvious to need elaboration. Of this map

¹ Publication No. 4 in this series.

2000 separate copies have been purchased; for more detailed work the Ordnance Survey 25 in. sheets, edition 1925, can be obtained.

The general scheme now in operation is briefly as follows: For each group worked the whole area is systematically surveyed, and the observed "presences" for each species in the group together with any information relating to habits, frequency, etc., are entered in a field note-book. From these data the observed distribution is plotted for each species on a separate map. On the wide left-hand margin, or otherwise attached to the map, are entered all relevant field notes with the dates upon which each record entered on the map was made. In certain cases, e.g. insects with aquatic larvae or nymphs, the imaginal and pre-imaginal distributions require separate mapping. Any reliable records previous to the date of the particular survey are also entered together with the source of the information.

These sheets, the map and the dated notes, thus give two sets of data—the distributions in space and in time during a given season. The accuracy of the latter set of data naturally depends on the length of the organism's active season and the frequency of the surveyor's visits. By the simple method of superimposing different maps over a "light-box" comparisons can be made of the distributions in space of (1) different species during the same season, and (2) the same species during different seasons. Comparison of the dated notes provides similar information in time.

For small organisms a different technique based on random sampling has to be adopted.

Botanically, South Haven Peninsula is an important locality for three reasons, all derived from the rare circumstances of its history. First, it affords most unusual opportunities for the study of plant establishment, plant succession and plant competition; secondly, it is specially suitable, owing to the comparatively simple and homogeneous nature of the substrate, for the investigation of the relationships between vegetation and edaphic factors; and thirdly, it has, taxonomically, a very rich flora including many rarities.

When the flora and fauna generally (or at any rate their principal components) have been mapped, several lines of further enquiry are open: (1) The comparison of maps, although not made in the same season, suggests correlations between organisms in different groups, and such apparently correlated species can then be simultaneously resurveyed with particular attention to the possible causes of association (e.g. the association of the grasshopper *Conocephalus dorsalis* with species of *Juncus*, the association of Conopid flies with Hymenoptera, the hawking sites of dragonflies in relation to their possible prey, the determination of the actual species eaten by phytophagous insects, etc.). (2) It is obviously impossible to present a complete picture of all the plants and animals as they are distributed in any one season, but if the various groups have been well mapped something approaching this could be attempted for small homogeneous parts of the area at particular seasons

of the year. (3) Possible causes of death and the incidence of the death-rate may be revealed by the comparative study of densities in different population centres and at different phases of the life cycle. (4) The presence or absence of a cyclical rise and fall in density and area of occupation can be tested by successive surveys of selected populations. (5) By catching and marking samples of animal populations it is hoped to determine the degree of individual movement within extensive continuous populations and between neighbouring discontinuous populations, and in this way to throw some light not only on the problems of colonisation and population movement but also upon the amount of germinal interchange.

The information to be gained by these methods may roughly be classed under four headings:

- (1) Individual life histories and autecological data.
- (2) Interrelationships within a complete society.
- (3) Colonisation and the limiting factors that govern the marked localisation of populations.
- (4) Population density, movements and germinal interchange.

In detailed mapping of this type it is essential that the surveyor of any group (other than those requiring microscopic examination or sampling treatment) should be, or before starting a particular survey should make himself, capable of recognising with certainty at least most of the prevalent species in his group when they are alive in the field. This necessitates, at any rate in some insect orders, the mapping of comparatively small homogeneous groups at any one period of working. Undiscerning mass collection may make dangerous inroads into populations of rarities or seriously disturb the natural balance of commoner forms, and thus some of the main objects of the survey would be defeated. On the other hand it is equally important that carefully controlled collections from at least the main centres of population must be made to support the taxonomic diagnoses even of the more stable well-demarcated species. In polymorphic and very closely related species the balance of safety between the preservation of the population and the collection of adequate material must be carefully judged. Arrangements will be made for the deposit of these collections together with the maps, field diaries and other records, if possible, at some central institution.

Efforts are being made to get air photographs taken, and it is hoped that this may be done at intervals so as to check with accuracy the rates of topographical and major vegetational changes.

A scheme of this sort must depend upon widespread co-operation. Any help or information will be welcomed. Among the more obvious needs are detailed analyses of soil and water, and studies of microclimates, but the main need is for specialists who are prepared to undertake the labour of making detailed surveys of their particular groups¹.

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We should like to take this opportunity of expressing our gratitude to Mr M. Hamilton Fletcher (who has the shooting and fishing rights over the Heath) both for his general kindness and help and for the trouble he has taken in finding the answers to difficult historical questions.

WORK NOW IN PROGRESS.

Plants. Vascular plants (R. D'O. Good: detailed species maps mostly remain to be done); Bryophytes (E. W. Jones); Myxomycetes (D. M. Cayley); Phytoplankton (B. Millard Griffiths); remaining groups not yet taken up.

Animals. Mammals (C. Elton); Birds (C. Oldham, K. B. Rooke); Reptiles and Amphibia (preliminary information only); Molluscs (C. Oldham, C. Diver); Insects: Orthoptera (C. and P. Diver); Odonata (C. Diver); Lepidoptera—Crambidae (C. Diver)—other families (preliminary information being collected from a number of sources); Diptera—Syrphidae and Conopidae (C. Diver, D. Aubertin); Hymenoptera—Aculeata (G. M. Spooner); Neuroptera, Mecoptera, Trichoptera (preliminary information—F. J. Killington, C. Diver); remaining groups not yet taken up.

Geology. Origin of the Dune Sand (D. Baden-Powell).

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A FIELD STUDY OF THE ST KILDA WREN
(*TROGLODYTES TROGLODYTES HIRTENSIS*),
WITH ESPECIAL REFERENCE TO ITS NUM-
BERS, TERRITORY AND FOOD HABITS

BY T. H. HARRISSON AND JOHN N. S. BUCHAN.

(With one Map and one Figure in the Text.)

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I. GENERAL.

ST KILDA is the name given to a group of islands (Hirta—St Kilda *sensu stricto*—Soay, Boreray and Dún) situated in the North Atlantic Ocean in latitude 57° 49' North, and longitude 8° 35' West. These islands, therefore, lie some fifty miles west of Harris and are the most western of all the Hebrides.

The evacuation of the island of St Kilda by its inhabitants in 1930 drew the attention of scientists to this isolated group of islands, and, in particular, interest was centred on the St Kilda wren protected by special Act of Parliament in 1904. With a view, therefore, of studying this bird, and carrying out other biological work, six scientists from the universities of Oxford and Cambridge stayed on St Kilda in the summer of 1931 from July 22nd to August 14th, with the permission of the late proprietor, Sir Reginald MacLeod of MacLeod, K.C.B. Permission for them to reside in the Factor's House was readily given by the late Mr John MacKenzie of Dunvegan. The party, in

addition to the authors, consisted of Malcolm Stewart, D. L. Lack, J. A. Moy-Thomas and C. P. Petch, and to these the authors wish to express their thanks for their helpful co-operation in connection with this paper.

Certain general papers on other ornithological subjects have already been published (2, 7, 8), and full reference should be made to these.

A Practical Handbook of British Birds contains but scanty information on the race, and much of this stands in need of modification and revision.

As early as 1698 Martin Martin in his classic *St Kilda* mentions the wren, as does Macaulay some sixty-six years later. In 1884 Seebohm (16) was the first to describe this bird as a new race (*Troglodytes t. hirtensis* Seebohm), from specimens collected by Dixon earlier that year. From that date onward this bird has always been in the public eye, and subject to persecution by collectors. It was the efforts of these people that caused W. H. Hudson to select a St Kilda wren, perched upon the skull of what appears to be a dodo, as the title-page of his *Lost British Birds* (11). Happily Hudson's pessimism was unjustified; but few birds have come nearer to extinction and yet survived to see better days.

II. PAST STATUS.

Till the year 1884, when Seebohm described this bird, it had always been common on the islands and was still so in 1885 when Charles Dixon saw it not only in the village area but also on the tops of the hills and on many parts of the cliffs. In the Rev. Neil Mackenzie's copy of his father's notes, 1829-43 (13), it is stated that there the wren was also resident. But within the space of four years collectors had reaped a ripe harvest and in 1888 the wren was almost extinct. In that year J. A. Harvie-Brown, in a bitter attack on collectors (he was himself a great ornithologist), wrote: "it is almost if not quite total extermination had been compassed in the short space of time between the announcement of its supposed specific identity and the present time." Adults, young, nests, eggs—all went into the cabinets.

Thanks largely to the efforts of Sir Herbert Maxwell, "The Wild Birds Protection (St Kilda) Act, 1904" was passed especially to protect the St Kilda wren and Leach's fork-tail petrel. This was just in time to save the remnant, for in 1895 J. Steele Elliott (6) wrote: "about fifteen pairs would fully represent their number on these islands now," and added that they were once far more numerous, and described how the eggs were sold to dealers. But thanks to statutory legislation, by 1910 the wren was again quite abundant, as recorded by Eagle Clarke, and in 1914 the Duchess of Bedford wrote that "several St Kilda wrens were noticed about the houses and cleits¹."

Since that time there has always been a good number breeding on the four main islands of the group, although it is apparently not so generally distri-

¹ A cleit is the name given to an oval dry-stone building used in the isles for the storage and drying of the peat, crops, etc.

buted as it was prior to 1885. This is no doubt due to the regular traffic in these eggs for many years. It is stated on the best authority that some five years ago as much as £5 was paid for a clutch, and the informant himself had purchased an egg for 7s. 6d., while he stated that a dozen or so nests were robbed annually.

III. 1931 CENSUS.

(a) *Numbers.*

Particular efforts were made with a view to obtaining an accurate count of the wren population during the observations of 1931, and the figures obtained are believed to be trustworthy. The count on Hirta was taken by both the authors and D. L. Lack, on Dún by Harrisson and Lack, and on the islands of Soay and Boreray by the former alone. Only pairs obviously in possession of territory and breeding were counted. Juveniles were excluded. The Boreray figure is, perhaps, too low, as only one observer was working, and it was only possible to stay on that island for some six hours. The results of the census are as under:

Island	Pairs	Acreage
Hirta	45	1575
Dún	11	79.4
Soay	9	244
Boreray	3 (?)	189.7
Total	68 pairs	

Dr A. M. Cockburn, who stayed some months in 1927 and 1928, has stated that he estimated under 100 pairs for the group; this roughly confirms the above figures.

Only on Hirta were there any birds nesting away from the cliffs, and these were connected with the village buildings. If pairs per acre on top, and per yard of coast-line are considered, the following results are obtained:

Island	Total acres per pair	Yards of coast-line per pair
Hirta	35	c. 410 (cf. Section III (c))
Dún	7	c. 560
Soay	27	c. 680
Boreray	63 (?)	c. 1400 (?)

From this it is apparent that there is no consistency in the distribution relative to total acreage, but that a consideration of number in relation to coast-line gives a good medium for comparison between the islands. Even allowing for possible error in the case on Boreray (see above) the density there was unexpectedly low in 1931. In 1885 Dixon (4) noted that the wren was especially common on Dún, and the high surface density of this island is due to it being composed of one large "puffin slope," unlike any of the other islands. Dr Eagle Clarke (3) stated that some bred on Stac an Armin, but he

did not visit the stac himself, and it was not possible for the authors to confirm his statement.

An examination of the distances between the nesting pairs will be found under subsection (c), while habitats—suitable and unsuitable—are considered below.

(b) *Habitats.*

The population, reckoned in 1931, of sixty-eight pairs may be divided into three well-marked habitats:

(1) Puffin slope; fairly accessible, irregular cliffs, with a thick vegetation of *Cochlearia anglica*, *Atriplex babingtonii*, *Matricaria maritima*, *Festuca ovina*, etc., upon which great numbers of puffins habitually nest.

(2) Steep cliffs; with a more scanty flora consisting for the most part of *Statice maritima* and various grasses and mosses. Upon these cliffs, which often grade into "puffin slopes," fulmars nest in large numbers.

(3) Buildings. These are used as nesting places only on Hirta, where about a dozen pairs nest in the village area, and one in a cleit on Ruaival. The large number of cleits and other buildings inland on Hirta, and also on the other islands, are not at present occupied by wrens.

Using the distinctions given above, the following figures are obtained:

	Pairs breeding on		
	Puffin slopes	Steep cliffs	Buildings
Hirta	24	9	12
Dun	7	4	—
Soay	5	4	—
Boreray	1 (?)	2 (?)	—
Totals	37	19	12

Total = 68

Thus 82 per cent. live on the cliffs and 18 per cent. away from the cliffs. These habitats, however, are not primarily botanical; for an ecological account of the flora see Petch (15).

None nested in the following habitats during 1931:

(4) Anywhere inland, except Hirta village.
 (5) Sheer cliffs which occur near sea-level and hold only auk and kittiwake colonies.

(6) Steep unbroken grass slopes with very few birds of any species.

There were also four cliff areas where wrens were scarce or absent, namely:

- (a) Ruaival. Low cliffs.
- (b) Oiseval. Low cliffs.
- (c) Glen Bay. Low cliffs.
- (d) West side of Glacan Chonachair. Apparently quite suitable.

Thus apparently in their present numbers they do not favour low cliffs. By far the greater part of the cliffs are between 600 and 1300 ft. high—

Conachair on the north side of Hirta being the highest cliff in the British Isles.

The presence of pairs in the village is closely related to the houses, as may be shown by taking three strip transects parallel with the village street:

	Pairs	No. of houses	Cleits
Between street and sea	1	—	c. 19
Along street	7	18	c. 40
Behind street	3	—	c. 70

The absence of any breeding inland is perhaps largely due to a scanty food supply; it certainly cannot be for lack of nesting sites, for the whole island is covered with cleits. It should be noted that individuals occur throughout the island in autumn (see section VII on Movements). Should the species at any time increase to any large extent it may spread inwards from the cliffs and village under pressure of numbers.

(c) *Spacial distribution on Hirta.*

One of the main features of the distribution of breeding pairs is the regularity of their occurrence in the favourable areas. Along the whole line of shelving puffin and fulmar cliffs, apart from the strips which are unsuitable for topographical or other reasons, wrens are to be found with regularity (see *Habitats*).

It was possible to obtain fairly trustworthy figures for distances between pairs on Hirta by using Mr Mathieson's excellent six-inch survey executed in 1928. Starting from Glen Bay and moving round anti-clockwise, the yard distances between the centres of activity (and presumed nest) of each pair are as follows: 450, 410, 400, 200, 150, 160, 170 (Geo na Stacan), 300, 330, 360, —, 200, 420 (St Brianan), —, 400, 190, 170, 200, 190, 230, 320 (The Gap), 370, 310, 200, 190, 230, 150, 170, 200, 210, 230 (Bradastac), 240, 150, 190. The blanks represent long unsuitable stretches. These distances should be compared with those of actual coast-line spacing in section III (*a*). The whole range of distance is 150–450 yards, and the number of nests at various distances increase as the distance becomes less, stopping suddenly at 150, thus:

5 cases of 400–450 yards separation.

6	„	300–390	„
10	„	200–290	„
11	„	150–190	„

The optimum density is therefore about 150–300 in suitable areas.

In the village there is the same regularity of distribution. The Factor's House, Manse and beach are rather isolated. The distances between pairs counting up the village are 200, 110, 95, 65, 75, 70, 80, 90, 170 yards. The average is rather over 90 yards, total variation 70–200. Only two village pairs are farther apart than the cliff minimum.

IV. TERRITORY.

(a) *New type of territory; food territories.*

In general the limit of the range of each pair was found to abut directly onto that of the next, but there was usually a "neutral zone" and a certain amount of overlap. On only one occasion was there observed an overlap of more than 15 yards (25 yards on August 10th). The distinction was, however, obvious even when young were present in the nest.

The size of a typical village territory was from about 3000-5000 square yards, but only a small part of this was used at all frequently. Usually most or all food was obtained within a small part of the territory. This was demonstrated by detailed observations over a period of a fortnight on a pair with small young in a cleit beside the Factor's House. Fig. 1 shows the dimensions of this territory and its relation to other pairs. The numbers represent "food areas" and these are discussed later.

From Fig. 1 it will be seen that only a small part of the area available to the bird is used for feeding purposes. Moreover, these "food areas" are small and separated from one another. Actual measurements are:

Food areas. Pair "A."

No. on diagram	Dimensions yards	Area sq. yards	Distance from nest yards
1	10 × 2	20	15
2	8 × 5	40	35
3	9 × 5	45	40
4	5 × 5	25	45
5	5 × 3	15	45
		145 sq. yards	

Of the whole territory of about 5500 square yards, only 145 (2.6 per cent.) were used during the fortnight of the observations. As shown in another section 85 per cent. of the food for the young was obtained in 1 per cent. of the area. Pairs "B" and "D" overlap slightly as indicated by the arrows, but pair "C" does not. The main feeding grounds are (1) and (2), and these are the closest to the nest, while about half the food is taken at 15 yards from the nest. As adults fly at about 12 m.p.h. they can reach the farthest corner of their territory in under 10 sec., which is essentially manageable. A great part of the territory is virtually unused, and one wonders if this is so in the case of other small passerines. If so, territory theories in general stand in need of serious modification.

(b) *Relations with other species.*

Wrens are commonly found breeding in the same habitat as rock pipits (*Anthus petrosus*), which are allowed to approach very close to the nest. Only once was any friction noticed, namely on July 30th, when a pipit was mildly attacked and driven off by a wren with young. On August 15th a juvenile

wheatear (*Oenanthe oenanthe*) and a small twite (*Acanthis flavirostris*) perched within a few feet of a wren's nest containing small young; the parents paid no attention. Pairs may often be found breeding among large colonies of fulmars (*Fulmarus glacialis*) and puffins (*Fratercula arctica*).

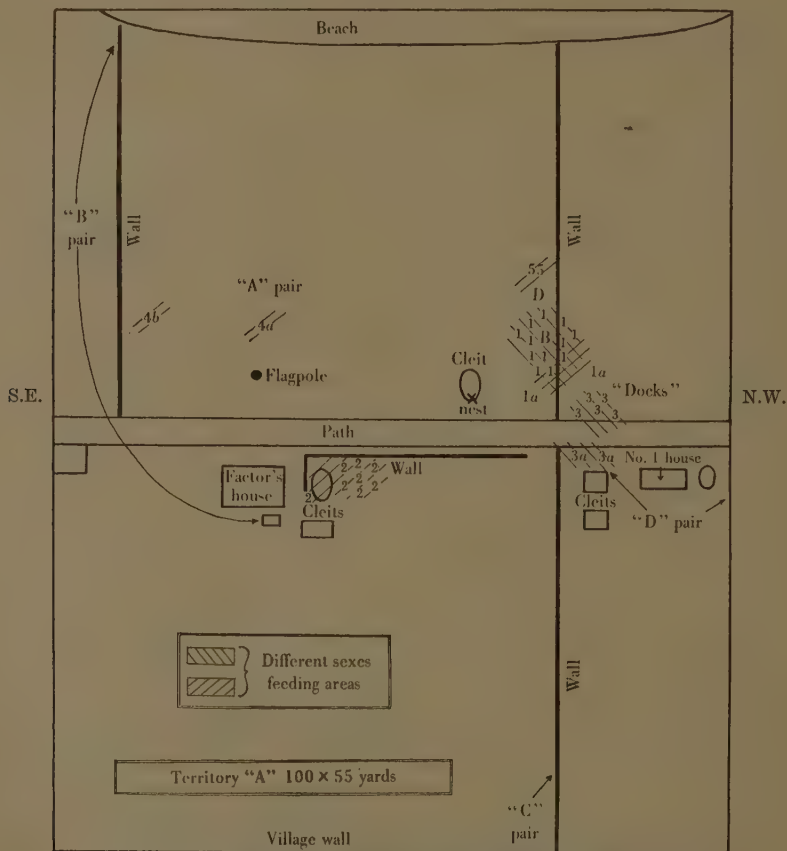


Fig. 1. Diagram of "A" pairs' territory (5500 sq. yards).

Seebohm (16), in his original account of the race, wrote that the wren "gradually acquired its grey colour and barred back by the slow process of protective selection, and is now almost invisible to the eyes of the hungry hawks that visit St Kilda." This charming passage must have been prompted wholly by imagination and current theories of evolution, for it must be quite exceptional for a wren to be taken by one of the three pairs of peregrines, the only "hungry hawks" on St Kilda.

V. Food.

(a) General.

According to *A Practical Handbook of British Birds* there is no definite information on food, but the wren "probably like the Shetland wren, picks up small Crustacea from the shore." This is certainly incorrect at the present time, for not a single bird was ever seen anywhere near the sea or even at the cliff base. As there are only four pairs nesting within a hundred yards of any sort of beach, it is quite impossible that any appreciable number live on Crustacea. Moreover, one pair nesting at the edge of the village beach fed exclusively inland. On the other hand, Dixon (4) "often saw it within a few feet of the sea" though he refers only to one or two pairs in the village bay area feeding on spiders and the larvae of different insects. Eagle Clarke (3) found that insects, almost entirely, were taken in September and October, and chiefly small beetles, but also flies, spiders, a few small seeds, and remains of vegetable tissue; no species are named.

In the village area birds were found to have travelled considerable distances to forage in beds of dry streams, and they showed a very marked preference for patches of dock (*Rumex obtusifolius*). Pairs with young in the nest took mostly green larvae of a Noctuid moth along with one or two Geometrid larvae, several centipedes, a few earwigs, and a number of spiders. The village adults themselves appear to feed largely on small beetles obtained from the base of the docks, and also spiders, centipedes and Thysanura. It is very unusual for village pairs to forage in the arable grassland which covers most of the area and has a particularly rich insect fauna living amongst the growth of *Holcus lanatus*, *Ranunculus acris*, *Anthoxanthum*, etc.

On six occasions adults were found feeding inside houses, including the Factor's House occupied by the party. They were apparently seeking Diptera and Thysanura.

Cliff pairs feed to a large extent on Diptera (Muscids) frequenting the rocks, and they also took a number of *Machilis* (abundant on the cliffs) and occasional Tipulids. Most of these were taken in crevices of the rocks or among the luxuriant patches of orach (*Atriplex babingtonii*) and scurvy-grass (*Cochlearia anglica*).

(b) Sex division of food territories.

Within the territory one bird uses patches quite separate from the other. In the case of the pair "A," kept under special observation, the two sexes each had two food areas exclusively their own, but one was used largely by "a" and occasionally by "b." In the diagram (Fig. 1) these food areas are numbered 1-4; (a) used only 1, 3 and 3 a; (b) only 1 (once or twice), 2, 4 and 5; thus out of thirty-two observations:

Areas on diagram	1	2	3 (and 3 a)	4	5	Total
Sex (a)	13	—	3	—	—	16
Sex (b)	3	11	—	1	1	16
Totals	16	11	3	1	1	32

So for sixteen records of each, in area 1 only three overlapped, the remainder being entirely separate for the two birds. Each has one main food territory where almost all food is taken, and one or two other areas visited much less frequently. (*a*) takes 41 per cent. at 1, and 9 per cent. at 3; (*b*) takes 9 per cent. at 1, 35 per cent. at 2, 3 per cent. at 4, and 3 per cent. at 5. The total overlap is therefore 9 per cent. confined to one area. Moreover, this overlap is confined to a third of this area (1 *a*), as indicated on the diagram. It is interesting to note that (*a*) takes all its food west of the nest, while (*b*) all but 9 per cent. east of it.

This division of territory into small food areas and still further into sex areas is very remarkable, and one cannot find that it has been observed in any other species. The division of labour between the two sexes has not been sufficiently considered. It is significant that in most cases where an intensive study of any one species has been taken some division has been demonstrated; e.g. the nightjar, where the male tends the first brood of young while the female incubates the second brood of eggs (12); the great crested grebe, where each adult tends to have its special young one for feeding purposes (9); and the house wren, where polygamy during nesting often occurs; the French partridge, woodpecker, etc. But though in these species and in some others, some form of sex division is well marked, this subterritory-food-sex division relationship seems to open up new possibilities. Maybe it occurs only in very sedentary, weak-flying groups like wrens; that remains to be seen.

VI. BREEDING SEASONS AND SIZE OF BROODS.

According to *A Practical Handbook of British Birds* the breeding season is "apparently June or July." This was confirmed by the present observations. The first lot of young were observed to leave the nest on July 30th (none before), when three were seen with their parents on Dún. Three young flew from nest IV when the nest was examined on August 2nd, and another brood of young flew 2 days later in the Glen. The eggs in nest V hatched on August 6th. The great majority of other pairs behaved as if with young in the nest, and this was confirmed by song periods and a song lull from July 27th to August 11th.

There were few signs of any first young having left the nest before the commencement of observations, or of a May brood. Only a fraction of the birds on the island were unpaired, and clearly all had nest territories. In 1931, at least, it seems fairly certain that most eggs were laid in early July. Steele Elliott found five fresh eggs on June 11th, 1894, a nest with one egg on June 12th and others added subsequently, and a nest with fresh young (and one added egg, sent to the Cambridge University Museum) on June 20th. These roughly correspond with the 1931 data. But Dixon (4) in 1884 considered that "its breeding season must commence early in May, for the young were three parts grown by the beginning of June." On this evidence the

species must be double-brooded, but detailed observations do not support this hypothesis, and none of the other passerines on St Kilda appear to be double-brooded. It is probable, however, that climatic conditions, especially humidity, may have an important local influence, and that there is a big difference between breeding dates in different years.

The average clutch is four to six eggs. In 1931 four young were found in one nest, but no broods of more than three flying young were seen, and there were several broods of one flying young only. Roughly, one young left the nest for every two eggs laid.

VII. MOVEMENTS.

In September and October 1910 and 1911, Eagle Clarke found scattered individuals all over Hirta, including the inland area of moorland, the beach, Great Glen, and elsewhere; no birds nest in these areas. Before the authors' departure in August 1931 there were signs of a similar movement. On August 2nd a single bird (probably juvenile) was seen high up on the hillside in the Great Glen, while on August 10th another single bird was seen on the Dún side of Ruaival. None nests in these places.

This autumn movement is slight enough, but indicates a tendency to move into non-nesting areas—into habitats which are not touched at all during the summer. It also suggests the possibility of wider movements, 50 or 60 miles to the Outer Isles. The common wren is known to be migratory to a marked extent, though it appears to be even more sedentary than the St Kilda wren. To quote *A Practical Handbook of British Birds* (vol. I, p. 495) on the common wren: "Passage movements along the east coast (Orkneys to Channel)...mid-September to mid-November and west coast (Hebrides to North Wales, and north, east and west coasts of Ireland), same period. Emigration from south coast England and Ireland with passage through Channel Islands...second week October to first week November. Weather movements in winter, Orkneys and Western Isles frequent." These movements must obviously affect, and no doubt include, the Shetland wren, Hebridean wren and St Kilda wren. Very important data would be obtained by intensive ringing of wrens on the Scottish islands and coastal mainland, for this is the only species with more than two races breeding within the British Isles.

This autumn movement has another important angle; it shows that the inland and other areas of St Kilda where no pairs nest can nevertheless support individual birds at other seasons. Lack of food is not the primary reason for non-nesting in these habitats.

VIII. MORTALITY.

While the party was on the island four dead birds were found; two in mouse-traps on the ground or in stone walls, one which had broken its skull by flying into a window, and one which had been killed by alighting in some tar on a hot day. There are now no birds or animals which feed on St Kilda

wrens; the few remaining semi-domestic cats were killed before departure. The egg traffic already mentioned has always been a check on increase, and now that the islands are uninhabited the birds may benefit. However, in the summers of 1932, 1933 and 1934 some islanders went back for a few months, and although Lord Dumfries, the present owner, employs a "bird-watcher" during the summer, the position is far from satisfactory. It would be much better if there was none there at all and the islands were left to themselves. The whole ecological experiment has already been damaged by allowing the islanders to go back each summer since the evacuation, the natural succession and modification of plant and animal life has been upset, and the whole success of the expedition at present stands in great jeopardy.

IX. SUMMARY.

1. The St Kilda wren (*Troglodytes t. hirtensis*) is confined to the St Kilda group of islands, some 50 miles out in the Atlantic. It was first described by Seebohm in 1884. At once collectors rushed for specimens, and in 1888 it was in danger of extinction. The Wild Birds Protection (St Kilda) Act, 1904 was passed to protect this bird, and subsequent increase occurred.

2. In 1931 a census was made on all the islands of the St Kilda group, and 68 nesting pairs were found in all; 45 on Hirta, 11 on Dún, 9 on Soay and 3 on Boreray.

3. These 68 pairs were nesting in the three habitats described; puffin slopes 37, steep cliffs 19, and buildings 12 (all these in the village on Hirta). 82 per cent. on the cliffs, but none nest on the large areas of moorland, hill-sides, etc. The optimum density along the cliffs is about 150-300 yards between nests, in the village 70-200 yards (average 90).

4. The average size of a territory in the village area is 3000-5000 square yards.

5. In one pair especially studied the territory was found to be composed of a number of subterritories, small areas in which food was taken. These food territories constituted only 2.6 per cent. of the whole territory, and 85 per cent. of the food for the young was obtained in 1 per cent. of the whole.

6. Food territories are further divided into sex territories, each parent tending to feed in exclusive food patches not used by the other.

7. Relations with other species are more or less negative.

8. Food is arthropodan, small beetles, flies, centipedes, earwigs, geometrid and other larvae, *Thysanura* and spiders in considerable quantities. Small seeds and vegetable tissues are also recorded.

9. Young were in the nest, hatching to flying, in August. There was no sign of an earlier brood.

10. Local movements to non-nesting areas take place in the autumn, while migration probably occurs.

11. Natural enemies are absent, with the one exception of man. The species will be best preserved by being left entirely alone.

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THE ARTHROPOD FAUNA OF A RICE-SHIP, TRADING FROM BURMA TO THE WEST INDIES

By J. G. MYERS, Sc.D., F.R.E.S., F.Z.S.

In July 1929 my wife and I travelled from Trinidad to Cuba by the S.S. *Chenab*, Captain Bryan, to whom I am indebted for very generous courtesies and facilities. The opportunity was taken, during the 13 days' voyage, to make a survey of the insects actually established on the ship. The material was kindly determined or checked by the Imperial Institute of Entomology. In all some forty-two species were collected.

The *Chenab* came from Calcutta, via Rangoon, with a large cargo of rice, chiefly from Rangoon, but some from Calcutta. She was fumigated at Calcutta with sulphur dioxide pumped in before the cargo was loaded, and then proceeded to Rangoon for the rest of the rice. At Trinidad she was fumigated again by the old-fashioned three-legged pan method, burning sulphur with methylated spirits. This fumigation lasted only six hours, and Captain Bryan informed me that *Ephestia* moths appeared in swarms in the cabins and companions next day. The decks were of "white pine" (*Pinus strobus*?).

Calls were made at Barbados, Santo Domingo, Kingston (Jamaica) and Havana. The ship docked only at Kingston, but no collections were made on port days save of insects actually in or emerging from the holds. The holds were opened at Santo Domingo and rice began to be discharged. Numbers of *Microbracon hebetor* were flying and crawling in the sun on the edges of the open hatches, also one specimen of a black Proctotrupid, slightly larger. In the evening more *Ephestia* than usual were in the dining-room and more *Tribolium* on the walls. No. 3 hold was examined with special care when it was partially opened to allow the entrance of men. The tiers of rice stacks were ventilated by hollow, open-work wooden prisms of an Indian wood somewhat like teak. This was largely unbored, save a few of the cross-boards, which showed "shot-holes." The borer was not found. The sides of the hold were lined with long slender bamboos, with a narrow lumen. These were taken on at Rangoon, and are made to last several voyages between India and the West Indies. Nearly all were badly bored, and the exit holes would have fitted the Scolytid collected in the same hold. None which I examined had beetles actually present, the worst being filled with empty frass and long since abandoned. In addition there were in No. 3 hold numbers of split bamboo mats (mostly from Rangoon), laid sometimes between sacks or wrapped round the iron pillars of the hold and placed up against the bamboo lining. In the latter case only were they bored with holes similar to those in the bamboo lining, and probably made by the emerging beetles. Elsewhere they were not attacked. When the lining of sticks has to be replenished at Calcutta instead

of Rangoon, bamboos are unobtainable or too dear, and fascines of miscellaneous exogenous sticks are used. A few of these lay in No. 3 hold, with the bark still adhering, but badly bored.

The very real danger of this "insect tourism" is shown by the fact that six days after reaching Havana, when we had travelled to the other side of the island, numerous live adults of the beetle, *Tribolium castaneum*, were found among our unpacked clothing.

There follows an annotated list of the Arthropods found on the *Chenab*, between ports or actually in the holds.

ORTHOPTERA.

BLATTIDAE.

Blattella germanica. Common, all instars running about, to a certain extent even during the day.

Supella supellectilium Serv. About the dining-room and the adjacent offices. Not so abundant as *Blattella germanica*. The pantry and gallery are the cockroach headquarters. Curiously enough there were very few among the rice sacks in No. 1 hold.

Periplaneta americana L. One specimen from forecabin. Much less abundant than *Blattella germanica*.

PSOCOPTERA.

Undetermined Psocid. A small, grey, wingless species running about among the debris under the sacks of rice in No. 1 hold.

HEMIPTERA.

Cimex hemipterus F. One specimen on my coat may have been gathered on shore in Kingston the previous day. Captain Bryan says it used to be very troublesome in the forecabin.

Undetermined Anthocorid. Two specimens in No. 3 hold. One on deck below bridge.

COLEOPTERA.

NTIDULIDAE.

Carpophilus dimidiatus F. Exact habitat not recorded. Not common.

TROGOSITIDAE.

Tenebroides mauritanicus L. In No. 1 hold during unloading of rice at Santa Domingo, always among rice and refuse or under bags on the boards, i.e. the lowermost sacks on that deck.

CUCUJIDAE.

Laemophloeus pusillus Schon. Exact habitat not recorded, though a number of specimens were represented in the collection.

Silvanus advena Waltl. In No. 1 hold, numerous among the floor debris and beneath the bags of rice. A few crawling on the latter. Plentiful in No. 3 hold.

Silvanus surinamensis L. One specimen stuck to paint on ventilator.

DERMESTIDAE.

Attagenus gloriosae F. On bunk in cabin, one specimen.

ANOBIIDAE.

Lasioderma serricorne F. A few in No. 3 hold. One in collected water below porthole.

BOSTRYCHIDAE.

Dinoderus minutus F. Exact habitat not recorded, but a number of specimens were taken.

Rhizopertha dominica F. Resting on walls. Scattered individuals in No. 1 hold, crawling on and under sacks of rice, with *Tribolium*. Plentiful in No. 3 hold. Several on deck below bridge.

TENEBRIONIDAE.

Tribolium castaneum Hbst. In cabin. Flying during the day and resting on walls. A few on deck below bridge. The most abundant insect in No. 1 hold, crawling about on the bags of rice. Plentiful also in No. 3 hold, on undisturbed sacks of rice. Infesting rice used at table.

BRUCHIDAE.

Bruchus chinensis L. On wall of passage near store-room; flying when disturbed, on walls near the open hold (at Santo Domingo). A few under sacks of rice in No. 1 hold. A few in No. 3 hold. Flying plentifully in the hot sunshine on deck.

Undetermined Scolytid. At entrance to No. 2 hold. Not infrequent.

CURCULIONIDAE.

Calandra sp. In rice used for the table. Plentiful.

LEPIDOPTERA.

PYRALIDAE.

Ephestia sp. Adults common on walls and ceilings. It has a common habit of clinging to isolated threads of Theridiid spider webs near the ceiling.

Undetermined moth. Resting on cabin door, one specimen. Larger than *Ephestia*, with maroon or wine-coloured wings pale on the costa. About 200 miles from Havana.

HYMENOPTERA.

EVANIIDAE.

Evania appendigaster L. On dining-table, one specimen. A well-known cockroach parasite.

BRACONIDAE.

Microbracon hebetor Say. Crawling on windows. Almost certainly parasitising *Ephestia* larvae. Less abundant in the hold itself than at the open hatches when rice was unloaded at Santo Domingo. It is strongly attracted to light.

PROCTOTRUPIDAE.

Undetermined Proctotrupid. On edge of the opened hatches, during unloading at Santo Domingo. Also down in No. 3 hold.

BETHYLIDAE.

Epyris sp. On upper windows. Scarce.

FORMICIDAE.

Paratrechina longicornis Latr. In cabins.

Ponera punctatissima Rog. At No. 3 hatch when it was partially opened to allow entrance of men.

Monomorium pharaonis L. Attracted by a bait of "Bemax" in our cabin. Occasionally in drinking water.

DIPTERA.

CULICIDAE, CULICINAE.

Culex fatigans W. Alighting on jam and bananas at table. One specimen. Two females swollen with blood in our cabin.

PIOPHILIDAE.

Undetermined fly. On soiled bedding of the pet kibibi (*Nasua nasua*).

MUSCIDAE.

Musca domestica L. Common.

MUSCIDAE, ACALYPTRATAE.

Undetermined fly. A small, black, sluggish species on banana on the dining table.

Undetermined fly. Ones and twos hovering over fruit and cheese on the dining table. Not common.

DROSOPHILIDAE.

Drosophila sp. On bananas on dining-room table. Scarce.

ANTHOMYIIDAE.

Fannia sp. One specimen in dining-room.

SIPHONAPTERA.

PULICIDAE.

Ctenocephalus felis Bouché. From pet *Nasua*.

ARANEIDA.

THERIDIIDAE.

Theridium sp. Built small irregular webs in ceilings.

Theridium sp. A red-legged species, very frequent. Egg cocoon a small, flimsy, slightly fluffy, pale greyish purple sphere, semitransparent, hung in the main web near the

female. This species catches *Ephestia* moths. Not infrequent in No. 1 hold, in the higher corners, but less abundant than the Pholcid species there. Also less common than in the pantry and neighbouring offices.

PHOLCIDAE.

Large spider. Common in No. 1 hold, where (and in Nos. 2 and 3) they were unloading rice at Santo Domingo. Thin irregular webs like those of *Pholcus phalangoides* in all the upper corners.

Large spider. With very banded legs, in captain's cabin. Male.

LYCOSIDAE.

Lycosa sp. One very active specimen on floor of dining saloon.

PSEUDOSCORPIONIDA.

Chelifer sp. In No. 1 hold among refuse and rice under the sacks.

N.B. It should be mentioned that none of the men were examined for lice, nor the few ducks, fowls, parrots and canaries for their special parasites.

APPENDIX.

Sarcophagidae and Muscidae on a passenger ship.

Bequaert (1926, p. 157) has elsewhere commented on the presence of Sarcophagids on passenger ships. In this connection the occurrence of the following flies caught at sea in a passenger ship proceeding in May 1930 from Trinidad to England, will be of interest.

Synthesiomys nudiseta Stein. Two days out from Barbados.

Sarcophaga aequata Wulp. About 300 miles past the Azores, at which we did not stop. Another specimen at sea opposite the Bay of Biscay, in cold weather.

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EPIDEMIC DISEASE AMONG VOLES (*MICROTUS*) WITH SPECIAL REFERENCE TO *TOXOPLASMA*

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(*With Plate VII.*)

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I. INTRODUCTION.

ALTHOUGH it has long been known that epidemic diseases occur among wild animals, very few serious attempts have been made to investigate them. This is largely due to the difficulty hitherto experienced in getting adequate contact between the laboratory and the wild animal. The effective study of epidemics among wild animals requires a special type of research organisation consisting of (1) a permanent and extensive field intelligence service to study fluctuations in numbers, evolve forecasting systems, and obtain material in the field; (2) a properly equipped pathological laboratory where almost any type of disease can be studied; and (3) a source of wild animals bred in captivity for controls and the experimental transmission of diseases¹. The inconclusive results of previous investigations have been due to the lack of one or other of these units. The present investigation is the outcome of a research organisation built up in the Bureau of Animal Population by Charles Elton, making available an effective field service and laboratory stocks of voles. At present the pathological work is being carried out with the co-operation of the Wellcome Bureau of Scientific Research.

¹ The technique of keeping and breeding voles in captivity is described in a paper by R. M. Ranson (1934), *J. Animal Ecology*, 3, 70-76.

We are indebted to the Forestry Commission, Liverpool Corporation and Messrs Bryant and May, who made grants to the Bureau of Animal Population in connection with field work and the maintenance of laboratory stocks of voles, etc. We should also like to acknowledge practical help in the field by the staff of the Forestry Commission, also by Mr E. H. Howard, Mr H. D. Jones and Mr D. K. McBeath. The experimental work would have been impossible without the aid of Mr R. M. Ranson in breeding laboratory stocks of voles at Oxford. We desire to thank Dr C. M. Wenyon, F.R.S., for his kindness in assisting in the identification of the toxoplasm here described.

II. EPIDEMICS AMONG MICE AND VOLES.

The causal agents of most epidemics among wild animals are still unknown, but it has been recognised that many outbreaks of disease take place at the end of a periodic increase in the numbers of the particular species involved. A short-period fluctuation associated with epidemics is known to occur among several species of mice and voles. As Elton (1931) points out, however, much of the evidence for epidemics is circumstantial, consisting as it does of records of enormous multiplication, followed by sudden decrease in numbers. Nevertheless, evidence is usually forthcoming that this decrease is not caused by migration, since dead bodies are often found with no marks of external injury. Records of such increases in numbers, followed by epidemics, cover a considerable number of years. Thus Patterson (1886) describes a mouse plague, followed by an epidemic, which occurred on a large scale in Nova Scotia (Canada) in 1815. The increase in the number of mice took place over an area of nearly 4000 square miles and was of much economic importance, since most of the hay and corn in the district was destroyed. In the autumn and winter the mice decreased in numbers rather quickly; they were seen crawling about in a languid manner and began to die in hundreds. In 1900 a vole plague broke out in Canada in the provinces of Saskatchewan and Alberta. Preble (1908) stated that immense numbers of the voles were found dead, their bodies floating down the rivers. A similar increase in the number of voles also occurred in 1907 in Nevada, Utah and north-western California. In the late autumn the fields were honeycombed with their burrows, but by August of the following year the voles had almost completely disappeared. Piper (1908), in recording this outbreak, states that, though dead and dying voles were reported at intervals from January to March 1908, all attempts to prove that the mortality was due to some specific bacterial disease were unsuccessful. Poison, however, could be excluded. Wayson (1927) also reported another great increase of mice in Kern County, California, in 1926-7. Though the species chiefly involved in the multiplication was the house mouse (*Mus musculus*), the vole (*Microtus californicus estuarensis*) also increased to a lesser degree. Later both species were found dying from a disease which was believed to be due to *Bacillus murisepticus*. The post-mortem appearances were

those of a septicaemia with purulent conjunctivitis, congestion of the vessels in the subcutaneous tissues, enlargement of the spleen and lymph glands, pneumonic patches in the lungs and white necrotic areas in the liver and spleen. Smears from the heart blood revealed a short Gram-negative bacillus.

In England the evidence as to epidemics in voles is somewhat scanty. One epidemic was noted by Moffat at the end of the great vole plague in Scotland, in the spring of 1893: "the voles seemed to get into a dormant state as if they were stricken by some disease...they disappeared underground, to be seen no more, where only a few days previously they had been running in thousands" (A. Moffat, cited by Middleton, 1930): another was reported among voles and long-tailed field mice by Dr T. G. Longstaff in the New Forest in 1923 (Elton, 1924). The first attempt on a comprehensive scale to study the health and parasites of a wild mouse population was made by Elton, Ford, Baker and Gardner (1931). Since there was evidence to show that 1926 would be a year of maximum abundance of wild mice in the south of England an intensive study was made of the mouse population in Bagley Wood, near Oxford. Although most of the work was focussed on the wood mouse or long-tailed field mouse (*Apodemus sylvaticus*) certain observations were made on the short-tailed field mouse or vole (*Microtus hirtus*). Since certain of these observations are of considerable interest in relation to our own experiments they may be briefly summarised: A *Microtus* (M4) died in convulsions on February 22nd, 1927. It had been in captivity for over a month, at the beginning of which period it had been used as an experimental animal and had received some sterile filtrate of human influenza sputum without showing any disturbance of health. Many other *Apodemus* and *Microtus* were dying spontaneously in captivity at this time. The brain of M4 was removed aseptically, emulsified and injected intraperitoneally into two other *Microtus* which had been observed for some time in captivity. One of these (M7) died on the sixth day, the other remained unaffected. The brain of the dead one was emulsified and injected (0.5 and 1.0 c.c.) intraperitoneally into two *Microtus* and two *Apodemus*, all freshly caught. The two *Microtus* died on the fifth and sixth days after injection, whereas the two *Apodemus*, injected with the same doses as the *Microtus*, survived without symptoms. Since no healthy control *Microtus* were available the experiment could not be continued. The brain of *Microtus* M7 was examined histologically but no lesions were found. Apart from this experiment neither bacteriological nor histological examinations threw any light on the cause of deaths in *Microtus*.

Since the termination of the work referred to above (Elton *et al.*, 1931) a study of British vole populations has been continued on ecological lines at Oxford by C. Elton, A. D. Middleton, and D. H. S. Davis. An intelligence service to keep track of the fluctuations in voles has been built up throughout Britain, and annual trapping censuses on standardised lines are now carried out on about forty representative areas. During the present century there

has been no widespread plague of voles in this country comparable with that which devastated the Lowlands of Scotland in 1890-2 or the plague in Southern England in 1814, but there has been a considerable number of outbreaks generally restricted to smaller areas. During the past twelve years these local plagues have often been of considerable economic importance owing to the extensive afforestation programme now being carried out by the Government. Newly planted forests on virgin land, particularly rough hill pasture in Wales, northern England, and Scotland, create exceptionally favourable conditions for voles. The exclusion of sheep and rabbits from these areas encourages a rank growth of grass and other ground vegetation on which the voles can be maintained at a much higher rate of population than on sheep-grazed unfenced ground. The periodic increases in the numbers of the voles naturally result in very high densities in some of these afforested areas, and in many cases a great deal of damage is done during the winter following a summer and autumn "peak" in numbers. The voles eat the bark of the young trees near the ground level, and with most species this results in the death of the tree.

In the Cowal district of Argyllshire (between Dunoon and Strachur), where extensive afforestation is in progress, there have been several noticeable peak years since 1920 resulting in a great deal of damage to trees. The peak years in this particular district have been 1922, 1926, 1929, 1932. In each case (particularly in the last three) damage was done to the trees by the abnormal vole population in the winter following the peak. (Voles do not breed from October to April.) Both in the spring of 1927 and 1930 the voles were observed to drop suddenly in numbers, and circumstantial evidence indicated that an epidemic disease was the cause of this reduction, although facilities were not available for an adequate pathological study.

III. THE EPIDEMIC AMONG VOLES IN 1933.

In Argyll the voles were very scarce indeed after the spring decrease of 1930, but they increased rapidly during 1931 and a great deal of damage was done to the forests during the winter of 1931-2. No reduction was noticed in the spring of 1932 and the summer breeding season resulted in a very high density. In view of the conditions existing in the autumn of 1932 it seemed very likely that a reduction in numbers due to disease would occur in the spring of 1933. After other plague years the reduction was usually noticed during March and April, but in this case the voles appeared to have decreased considerably in Argyll by the end of January 1933, so the actual date of the onset of mortality is uncertain. When trapping in Glenfinart during February 1933, it was difficult to find live voles although the ground appeared to have been infested with them just previously.

In the forestry plantations around Lake Vyrnwy, North Wales, voles were also in high numbers and doing a great deal of damage during the winter 1932-3; and no signs of a reduction in numbers were observed before the end

of February 1933. The past history of the Lake Vyrnwy vole population was not so fully known as that of Argyll, but it seemed probable that an epidemic might occur in the spring of 1933. Several other afforested areas in Scotland were found to have abnormal numbers of voles at this time.

Accordingly, efforts were made to get regular supplies of live voles from Argyll and Lake Vyrnwy during March and April 1933, while a certain number were also obtained from other areas where there seemed a possibility of disease breaking out. The Forestry Commission and Liverpool Corporation (Lake Vyrnwy) provided labour and every possible assistance in getting voles sent alive to London. In Argyllshire the numbers had already fallen so low that it was found impossible to get the proposed quota of ten live voles per week; but trapping was carried on continuously and all voles caught were sent to London. The procedure adopted was, briefly, as follows: the voles were caught alive by a variety of methods which need not be described here, and sent as quickly as possible to London by rail in roomy well-ventilated boxes supplied with a large amount of their natural food and nesting material. Actually, no deaths occurred on the journey from any of the trapping centres, although the voles sometimes had to travel for 24 hours. At Lake Vyrnwy, trapping was comparatively easy, and the weekly quotas of voles were usually received in London the same day as caught. In Argyll, voles were collected until about 6-10 could be sent off at once, some of the voles, therefore, being in captivity for 3-5 days before reaching London.

On arrival at the Wellcome Research Institution the voles were carefully isolated and kept in separate cages on a system which has been proved successful for keeping ordinary wild voles and breeding them in captivity at Oxford. Mortality due to conditions of captivity or unnatural food may, therefore, be regarded as negligible for the period of observation. The voles were watched carefully and examined when they died. Voles were bred in captivity at Oxford from a laboratory stock which had been successfully bred for two years. Supplies of these voles were sent periodically to the Wellcome Institution for use as controls and carrying on serial passage. Strict precautions were taken to ensure that no contamination of the Oxford stock should occur; no voles were brought to Oxford from any outside areas during the period of investigation. In the table is shown the history of sixty-three voles which were examined after death in London, in nineteen of which *Toxoplasma* was found. This probably does not represent the total number which harboured parasites, for of the forty-four other animals many died during the night and on examination were too decomposed to afford accurate data.

A careful watch was kept for any dead or diseased voles on the several areas concerned and any found were sent immediately to London.

In Argyllshire the vole population was reduced to a very low level by the epidemic, so that it was practically impossible to catch a vole on the forestry plantations at any time during the summer of 1933. At Lake Vyrnwy, however, the mortality which started in March did not continue, and, although

the voles were greatly reduced at that time, they increased again throughout the summer of 1933. In October 1933 the vole population at Lake Vyrnwy appeared to be nearly equal to that of the corresponding period in 1932, but by March 1934 the numbers were down to a very low level.

Results of examinations for Toxoplasma of voles dying in London.

NORTH WALES.					
Date received	No. of days before death*	Presence of toxoplasms	Date received	No. of days before death*	Presence of toxoplasms
1. iii. 33	6	d.	9. iii. 33	8	+
"	7	+	"	9	d.
"	7	d.	"	10	+
"	8	-	"	10	+
"	17	d.	18. iii. 33	5	d.
8. iii. 33	4	-	28. iii. 33	2	d.
"	5	+	"	3	-
"	6	+	"	5	+
9. iii. 33	7	d.	"	23	+
"	7	+			
ARGYLL.					
5. iii. 33	3	+	25. iii. 33	3	d.
"	3	+	"	3	d.
"	4	d.	"	3	-
"	6	d.	"	3	-
"	11	d.	"	3	-
15. iii. 33	5	-	"	3	+
"	5	-	"	3	-
"	7	d.	"	3	+
"	7	d.	"	4	d.
"	7	d.	"	4	+
"	7	d.	"	4	+
"	8	+	"	6	+
"	8	d.	2. iv. 33	2	d.
"	9	+	"	2	-
"	9	d.	"	2	d.
"	9	-	"	2	d.
"	9	-	"	3	-
"	9	d.	"	8	-
"	9	+	"	8	+
"	9	+	"	8	-
"	16	d.			

+ = *Toxoplasma* found on post-mortem.

- = No *Toxoplasma* found.

d. = Too decomposed for examination.

* Dated from day of arrival in London. Some of the Argyll voles were caught as much as 5 days before and housed temporarily in the field before transit.

Unfortunately many of the voles died during the night, having been in apparently good health on the previous evening, so that no clinical symptoms could be noted: however, in more than twenty voles kept in the laboratory definite clinical symptoms were observed while similar symptoms were also observed by one of us (A. D. M.) in the field at Lake Vyrnwy. The first appearance of ill health was a slight sluggishness in movement, the eyes being less prominent than usual. This lethargic period was quickly followed by one of convulsive activity. The voles exhibited head retraction, circular movements, hunching of the back, and frequently paralysis of the hind-limbs, associated with periodic convulsive movements. Sometimes sudden death occurred

during these convulsions, more commonly the voles passed into a comatose condition, followed after a short period by death. These symptoms, which strongly suggest cerebral irritation, are, it is interesting to note, similar to those observed by Elton, Ford, Baker and Gardner (1931) as occurring in a vole during the 1926-7 investigation. Symptoms of this nature were observed in voles within twenty-four hours of arrival in the laboratory, and up to as long as five months after arrival. The voles were carefully isolated on arrival and thus did not come in contact with other laboratory animals, in which similar symptoms were not observed. This fact combined with the observation of cerebral symptoms in voles in the wild state is not in favour of the view that the voles contracted any disease from other laboratory animals.

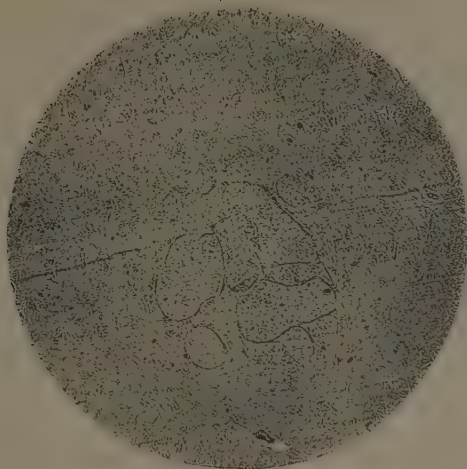
IV. THE CAUSE OF CEREBRAL SYMPTOMS IN *MICROTUS*.

As soon after death as possible all voles were carefully examined. The internal organs in all animals were entirely normal in appearance with the exception of occasional cysts in the liver due to the larval tapeworm *Taenia tenuicollis* Rudolphi. Bacteriological cultures of heart blood, spleen and liver in a number of media were invariably sterile, except for the rare appearance of obvious post-mortem contaminants, while films of heart blood, liver and spleen also failed to disclose any obvious parasitic infection. Histologically also, liver, lungs, spleen and kidneys appeared normal. In the brains of some animals there was noted, however, a slight increase in the number of the cells of the lymphocyte series present in the meninges, but no definite perivascular infiltration in the substance of the brain itself. It was at first thought that possibly the cause of death was due to an ultramicroscopic virus with neurotropic properties and, since the cerebral lesions produced by such viruses may in certain instances be patchy in distribution, serial sections were cut of a number of vole brains. No histological evidence suggestive of a virus infection was discovered but cysts of a toxoplasma were found, irregularly distributed in the brain substance.

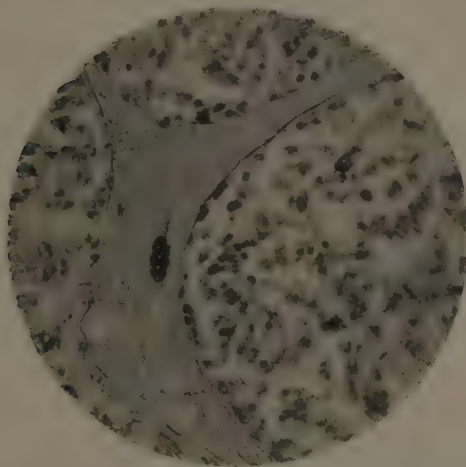
Parasites of the genus *Toxoplasma* are a little understood group of Protozoa, usually placed in the class Sporozoa, near the Piroplasmidea.

As a result of this discovery very careful inspection of the brains of voles dying with cerebral symptoms was made, and in the majority of the brains it has been possible to detect the presence of the cysts with a hand lens as very minute, pale, rather translucent areas in the brain substance. The distribution of the cysts is very irregular: they are found most commonly in the cerebral lobes but have also been encountered in the cerebellum, mid-brain, pons and medulla.

The cysts which seem to arise from the dilation either of endothelial cells lining the small capillaries or of neuroglia cells frequently appear in cross-section multilocular. The actual cysts vary from 0.2 to 1.0 mm. in diameter and are bounded by a definite membrane. They cause little or no reaction in



Phot. 1. Toxoplasma cysts in the brain of *Microtus*: reaction on the part of the nervous tissues is absent: stained Mayer's acid haemalum and eosin. $\times 25$.



Phot. 2. Toxoplasma cysts in the brain of *Microtus*. The actual toxoplasms can be seen in the cysts, which are lined by a definite membrane: stained Mayer's acid haemalum and eosin. $\times 1000$.

the surrounding brain tissue, which is merely pushed aside by the slowly dilating cysts (Pl. VII, phot. 1). The interior of the cysts is filled with hundreds of toxoplasms which are indistinguishable morphologically from those described by other observers. In shape the individual toxoplasms are falciform, one end being rather more rounded than the other. The nucleus is as a rule eccentric, though very rarely it may be centrally placed. The average dimensions of the toxoplasms is $4.6 \times 1.5\mu$ (Pl. VII, phot. 2)¹.

V. TRANSMISSION EXPERIMENTS WITH *TOXOPLASMA*.

Although the brain is the only organ in which toxoplasms have been found, the parasite is also apparently present in the peripheral blood stream, since positive results have been obtained following inoculation with blood. Transmission experiments have been carried out both by intracerebral and intraperitoneal inoculation, though results have been more consistent when the former mode of injection has been used.

The following protocols are illustrative of the results obtained by passage in voles:

23. iii. 33. Argyll vole found in a drowsy condition: killed, heart blood sterile, 0.3 c.c. inoculated intraperitoneally into two normal Oxford voles. One vole found dead and eaten 10 days later, the other developed nervous symptoms 32 days later: killed on 24. iv. 33, blood sterile: 0.3 c.c. inoculated intraperitoneally into two normal voles. One found dead 7 days later, the other developed nervous symptoms. 2. v. 33, killed and blood inoculated as before into two normal voles. One vole died 9 days later with nervous symptoms, the other survived. Toxoplasms present in brains.

With vole brain several serial passages have been made.

8. iii. 33. Brain removed from Welsh vole with nervous symptoms: 0.03 c.c. of a 1 in 10 dilution of brain in saline inoculated intracerebrally into two normal voles. These died 7 and 8 days after inoculation. Toxoplasms present in brains.

Brain removed from one of these voles inoculated as before into two voles which died 7 and 10 days after inoculation. Brain removed from vole dying on seventh day after inoculation again inoculated intracerebrally into two voles which died with nervous symptoms 8 and 11 days after inoculation. Toxoplasms present in brains.

A limited number of experiments have been made on the transmission of the vole toxoplasm to other species. These show that guinea-pigs and rabbits inoculated intracerebrally develop a meningo-encephalitis due to *T. microti*, death occurring in from 8 to 15 days. In white mice it has not been possible to produce an acute encephalitis, although a few mice died 20–30 days after inoculation with more chronic lesions. Similar results have been obtained on inoculating *Apodemus sylvaticus*. These animals killed 30 days after intracerebral inoculation exhibit no definite cerebral changes though their brains are apparently still infected with toxoplasms as shown by inoculation into voles. Injections made with emulsions of brains of voles of blood passed through Seitz or Berkefeld filters were invariably negative.

¹ *Toxoplasma* cysts were found in the brains of animals dying with nervous symptoms in the field and in the laboratory but not in control voles from Oxford.

VI. CEREBRAL LOCALISATION OF TOXOPLASMS IN OTHER SPECIES.

During the past few years a number of observers have described toxoplasms in the brains of various animal species. Thus Arantes (1914), in studying the results of inoculating *Toxoplasma canis* into the pigeon, found that large numbers of parasites were present in the brain where they formed cysts. Levaditi, Sanchis-Bayarri, Lépine and Schoen (1929) also found that strains of *T. cuniculi* from the rabbit gave rise to an acute encephalomyelitis in rabbits, guinea-pigs, and pigeons. In mice and rats the lesions were of a more chronic character. Recently Levaditi and Schoen (1933) have described a toxoplasm in the brain of a baboon (*Cynocephalus babuin*) which had been inoculated intracerebrally with the lymphatic glands of guinea-pigs, although monkeys are as a rule very resistant to intracerebral inoculation with the usual strains of *T. cuniculi*.

Coutelen (1932, 1) described the occurrence of a toxoplasm, *T. wenyoni*, in the brains of two Mitchell's wombats (*Phascalomys mitchelli*) from the Gardens of the London Zoological Society. These animals, according to Hammerton (1932), exhibited nervous symptoms not unlike those described in voles. Coutelen (1932, 2) also described cysts in the brains of ferrets due to *T. laidlawi*. These ferrets had been bred under conditions of strict isolation. Finally, Nicolau (1932) has described brain lesions due to spontaneous infections in guinea-pigs with *T. caviae* (Carini and Migliano), while Nicolau and Balmus (1933) have reported similar spontaneous infections in the mouse due to *T. musculi* (Sangiorgi).

It is noticeable that all the descriptions of toxoplasmic infection of the brain so far described have been found either in laboratory animals or in those living under somewhat artificial conditions in Zoological Gardens. Even in the case of the gundi, *Otenodactylus gundi*, the first species for which a toxoplasm was ever described, Nicolle and Manceaux (1908) could only find it in animals kept for some time in the Institut Pasteur of Tunis: newly caught animals were invariably not infected.

The finding of a toxoplasm in the brains of newly caught voles thus appears to be the first instance in which these organisms have been detected in animals living under entirely natural conditions. Although it seems not improbable that the various types of toxoplasms so far described in various animal species may be referable to one or perhaps two species yet in the present uncertain state of our knowledge it seems advisable, as has been customary in the past, to apply a specific designation to each toxoplasm isolated from a new host. We therefore propose the name *Toxoplasma microti* n.sp. for the toxoplasm parasitic in the field vole *Microtus agrestis*.

VII. DISCUSSION.

Observations on voles from Argyllshire and from North Wales during a period of mortality failed to disclose any bacterium or ultramicroscopic virus as a cause of death. The only explanation of the nervous symptoms occurring before death was the presence of cysts of a *Toxoplasma* in the brain. Elton, Ford, Baker and Gardner (1931), it may be recalled, also described nervous symptoms preceding death in a vole from Oxford. Thus, although it is quite possible that vole populations may be attacked by other infections it will be necessary in future epidemics to take into account the possibility of infection by toxoplasms, as these organisms would seem to be widely distributed in voles living under natural conditions.

The natural method of spread of the toxoplasmic infection in voles has not yet been definitely determined. Two possibilities suggest themselves: (1) transmission by ectoparasites; (2) contamination of food. Three attempts were made to transmit the toxoplasm infection by inoculating subcutaneously ectoparasites from voles dying with *Toxoplasma* cysts in the brain. The ectoparasites consisted chiefly of *Ctenophthalmus agyrtes celticus*, though some other species of flea may have been present. These experiments were unsuccessful. On the other hand, Nicolau and Balmus (1933), in the case of mice infected with *Toxoplasma musculi*, have occasionally found cysts in the kidneys, while Coutelen (1932, 2) noted a small cyst in the intestine of a ferret infected with *T. laidlawi*. Experimentally it has been possible to transmit *Toxoplasma* infections to guinea-pigs and rabbits by feeding them by mouth with food contaminated with toxoplasms. The evidence therefore suggests that in all probability the infection is transferred in the case of voles by contaminated food. The great increase in the numbers of field voles which periodically occurs would provide very suitable conditions for this method of spread to cause widespread epidemics.

In view of the paucity of our knowledge of the toxoplasm group it is hoped that more intensive experimental work, both in the laboratory and in the field, can be carried on with *T. microti*. Since the natural mode of infection of *Microtus* has not yet been determined, it is difficult to say whether this organism might be safely and usefully applied to control excessive increases of voles in forestry plantations—which is a very desirable objective. The probability of infection through food contamination or via ectoparasites, however, makes it appear profitable to pursue the subject of deliberate infection of the voles at their peaks in numbers. If the epidemics could be started in early autumn the damage to trees would be obviated, since it occurs only during the winter months. In any case the disease cannot be tried out in the field until its pathogenicity to other wild and domesticated animals has been tested experimentally.

VIII. SUMMARY.

During a period of mortality among wild voles, *Microtus agrestis*, in Scotland and North Wales, the only apparent cause of death has been the presence of cysts of a toxoplasm (a parasitic protozoan) in the brains of the voles. This toxoplasm is described as *Toxoplasma microti* n.sp. It has been possible to transmit the toxoplasm to healthy voles and to guinea-pigs and rabbits by means of brain emulsions and heart blood.

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THE PART PLAYED BY ALTERNATIVE HOSTS IN MAINTAINING THE TICK POPULATION OF HILL PASTURES

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(With one Figure in the Text.)

I. INTRODUCTION.

PARASITES in general have a fairly specific host relationship, in that their host range is limited to one species in extreme cases, or, more commonly, to two or more nearly related species. In the absence of the normal host or hosts, the parasite will not, or cannot, adapt itself to other hosts. It is recognised, however, that certain parasites are less highly specialised, in that this specificity is less marked, and they are able to support themselves with more or less success on secondary or alternative hosts.

The importance of the question of alternative hosts is obvious in the case of parasites of economic significance, since it is clear that the facility with which a parasite can be eradicated will vary inversely with its adaptability to hosts other than the normal one. A modification of the same problem is presented by the survival of trypanosomes in the natural reservoirs represented by wild game, which act as alternative hosts for the vectors which transmit these same trypanosomes to domestic animals. It is apparent that this aspect of the ecology of parasites is of very considerable importance, and deserves greater attention than that so far devoted to it.

The writer is unaware of any studies of a quantitative nature on the part played by alternative hosts in perpetuating parasitic species, although many lists have been given of the possible alternative hosts for different parasites.

In the following work, which forms part of a general investigation of the bionomics of *Ixodes ricinus* L., the common tick of Britain, a qualitative and quantitative analysis has been made of the part played by wild mammals and birds in supporting the tick population of hill pastures.

II. HOSTS OF *IXODES RICINUS*.

A study of the possible hosts of *Ixodes ricinus* was made, the detailed results of which have already been recorded (MacLeod, 1933). It appears, from the writer's findings and those of other workers, that one or more stages of the tick could survive on the following warm-blooded hosts: *Mammals*: horse, cattle, deer, hedgehog, dog, fox, cat, stoat, weasel, ferret, hare, rabbit, rat, squirrel; *Birds*: siskin, hoodie crow, jackdaw, golden plover, kestrel, merlin, sparrowhawk, barn owl and grouse.

The great scope of this host range is of interest. It is important, however, to determine the extent, if any, to which a tick population can be supported in the absence of the sheep host, for the mere fact that occasional ticks may feed on the above alternative hosts is no proof that they could be maintained in any numbers if they were entirely dependent on hosts other than the sheep.

III. THE EXPERIMENT.

In the following experiment an area of tick-infested pasture in the Ettrick valley was separated from the rest of the farm. The original sheep-supported population of ticks was reduced until the only ticks present were those which had succeeded in surviving on alternative hosts. The method used was as follows. A 10-acre plot of typical hill pasture was fenced off in May 1929. This was surrounded by a "neutral area," 45 yards broad, to prevent unfed ticks crawling in from the surrounding pasture. The outer fence consisted of game-proof wire netting of $1\frac{1}{2}$ in. mesh, so that only the smaller forms of mammalian life could obtain ingress. It is known, however, that hares succeeded in entering the area by leaping the boundaries. The original tick population was eradicated in the following manner. A dipping tank was constructed in one corner of the enclosed area. Twenty-one sheep were dipped to free them from attached ticks, and liberated on the central area. They were dipped every fifth day for several weeks, and then removed. In the autumn of the same year, forty-two sheep were grazed on the area and dipped every third day for six successive dippings. This procedure was again repeated in the autumn of 1930, twenty-six sheep being dipped at three-day intervals for five successive dippings. In this manner, the number of ticks was steadily reduced, those which attached themselves being killed by dipping before they could complete engorgement. Care was taken to prevent extraneous contamination of either the central or neutral area: the sheep were transported in and out in a specially constructed solid walled carrier, and the experimenters were required to wear rubber knee-boots, which were washed in a tub of insecticide, placed immediately inside the outer fence. After September 1930, the area was left vacant until the spring of 1932. Thus, from May 1929 until the beginning of the tick season of 1932, no ticks in the central area were able to feed on sheep and drop back on to the pasture. The individuals of the original tick population, *except those which fed on alternative hosts*, were either removed and killed by the repeated serial dippings, or starved to death for want of a blood meal.

At the end of September 1930, when the area had been subjected to three spells of intensive stocking and serial dipping, the number of ticks was considered to have been reduced to a minimum. For the succeeding eighteen months, the area was left untouched, to allow of the vermin- and bird-supported population attaining an equilibrium.

IV. RESULTS OF THE EXPERIMENT.

About the middle of April 1932, ten sheep, after being carefully dipped, were placed on the central area. Accurate counts were made every fourth or fifth day of the number of female and nymphal ticks attaching themselves to the head, neck and ears of five of these sheep. As a control, similar counts were made of the degree of infestation of twelve of a group of sheep pastured on the adjacent areas of tick-infested pastures. The results are shown in the table, and the comparative degrees of infestation per sheep in the two groups are represented in the accompanying graph (Fig. 1).

It will be seen that, although the degree of infestation was markedly

*Comparative degree of infestation of sheep on experimental area
and ordinary farm grazing.*

Date	Controls				Average per sheep	Experimental area				Average per sheep
	No. of sheep examined	♀♀	Nymphs	Total		No. of sheep examined	♀♀	Nymphs	Total	
16. iv. 32	12	16	72	88	7	5	—	1	1	—
21. iv. 32	12	17	180	197	16	5	6	5	11	2
25. iv. 32	12	34	89	123	10	5	2	3	5	1
1. v. 32	12	50	180	230	19	5	10	23	33	6½
5. v. 32	12	31	98	129	11	5	9	18	27	5½
9. v. 32	12	42	204	246	21	5	2	2	4	1
14. v. 32	12	42	204	246	21	5	3	18	21	4
18. v. 32	12	72	468	540	45	5	2	20	22	4½
23. v. 32	12	56	204	260	22	5	4	24	28	5½

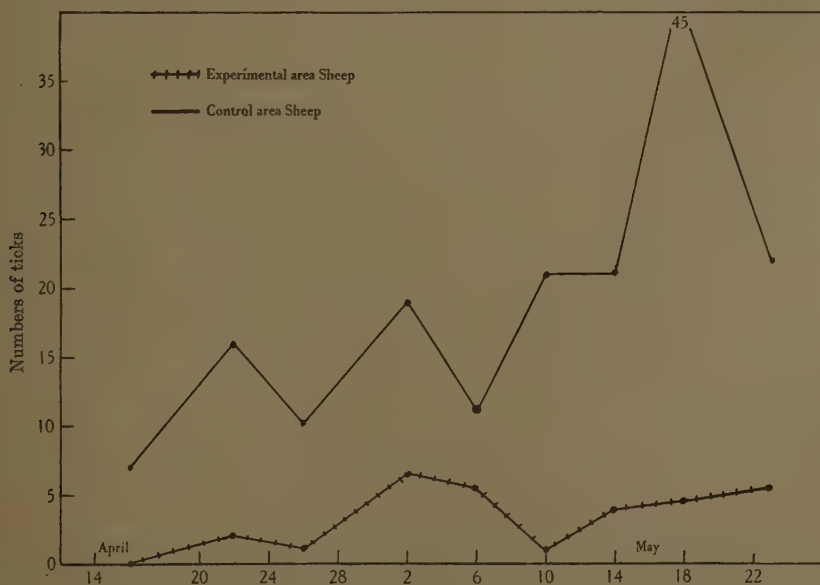


Fig. 1.

greater in the sheep grazing on the ordinary pasture, there was a regular and appreciable infestation of those sheep on the central area. The average degree of infestation of each group may be taken as a reflection of the comparative density of the tick population of the central area and of the ordinary pasture. The comparative density of stocking of the two areas during the experiment, although it would affect the result in the next generation of ticks, does not affect the immediate result, since a grazing sheep covers in a day a constant area of pasture irrespective of the density of stocking, and so the average infestation per sheep will remain constant. It would appear, therefore, that in the central area a tick population of appreciable size was maintained by ground vermin and birds, although no ticks on this area had engorged on sheep for the previous three years.

This result, apart from its important bearing on tick control measures, is of interest in that we have here a parasite which, although normally affecting one chief host, is able to maintain itself in appreciable numbers in the complete absence of that host. The result is the more striking in that the number of possible alternative hosts was very much reduced. Hares obtained access by virtue of their leaping powers; apart from them, the only mammals likely to have gained entry, and which are known to harbour ticks, were weasels and stoats. It is not known whether these ticks feed on mice and voles. The only other possible hosts were the common moor birds.

It is probable, therefore, that many of the more adaptable parasites with a comparatively wide host range are able to survive in the complete absence of their chief host or hosts.

V. SUMMARY.

1. The sheep tick, *Ixodes ricinus*, feeds on a very wide range of hosts other than the sheep. As shown in a previous paper, these include the horse, cattle, deer, hedgehog, dog, fox, cat, stoat, weasel, ferret, hare, rabbit, rat, squirrel, hoodie crow, jackdaw, golden plover, barn owl, grouse, kestrel and merlin hawk. Since then, it has been recorded from the siskin and sparrowhawk, (Thompson, 1934).

2. In a 10-acre area, from which sheep were excluded, a tick population of appreciable extent was maintained where the only available hosts were birds and hares, and ground vermin such as field mice, voles, weasels and stoats.

3. The effect of these alternative hosts on the population was allowed to operate over a period of eighteen months before the density of the population was estimated.

4. It would appear, therefore, that in the case of *Ixodes ricinus*, removal of the chief host (sheep) from a particular area for a number of years would not effect the eradication of the parasite from that area.

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STUDIES OF FLUCTUATIONS IN INSECT POPULATIONS

III. THE GALL MIDGE, *RHABDOPHAGA HETEROBIA* H.L.W.,
ON BLACK MAUL VARIETY OF *SALIX TRIANDRA*
AT SYSTON, LEICESTERSHIRE, 1927-33

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(With four Figures in the Text.)

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I. INTRODUCTION.

THIS is the third of a series of papers giving the results of an attempt to study fluctuations in insect populations as they occur in nature. The first study (1) was concerned with the wheat blossom midges on an experimental field (Broadbalk) of permanent wheat at Harpenden, Herts. The second (2) dealt with the infestation of wild meadow foxtail grass (*Alopecurus pratensis*) near Aberdeen by the gall midge *Dasyneura alopecuri* (Reuter).

In the present contribution an account will be given of the "button top" midge or *Rhabdophaga heterobia* H.L.W., as it has occurred in a bed of commercially grown Black Maul (*Salix triandra*) basket willows near Syston, Leicestershire, during the past six years.

Mr A. Roebuck of the Midland Agricultural College has very kindly written a paper (12) to accompany mine, in which he gives a general account of the particular willow beds from which material for this study has been obtained. He has pointed out how the species studied has been carefully nursed so that it is always present in immense numbers, whereas there are other insects which have fared worse against flood and rain, etc. After dealing with the

other pests, he explains how a change in the method of working the beds would have probably prevented my study from being made.

The previous studies are resembled in so far that the degree of parasitism of the midge and the dates of emergence of the adult midges have been studied. But the varying extent of infestation of the crop has not been considered in any detail.

It should be pointed out that, whereas in the two previous studies each successive brood of the insect has been considered (the midges in question being normally single-brooded), in the present instance each over-wintering brood only has received attention. The intervening broods have not been studied, except under experimental conditions (see section III).

II. METHODS.

The method of sampling has been reduced as far as possible to a maximum of simplicity. Once a year, at the very end of October or beginning of November, a visit has been made to the Wanlip willow beds near Syston, Leicestershire. On November 1st, 1927, a single sample¹ of 500 "buttons" or galls caused by the larvae of *R. heterobia* was collected during the process of wandering to and fro over a single field in such a manner that the whole of the field was traversed. The same procedure was followed on October 31st, 1928. On October 30th, 1929, however, three separate samples of 500 galls were collected in the same manner, each sample being kept as a unit. On October 31st, 1930, 1500 galls were collected and subsequently mixed and divided into three samples of 500 galls. In 1931 (30. x. 31) and 1932 (1. xi. 32) this same procedure was used. In each year the samples have been brought back to Rothamsted Experimental Station and kept continuously in an outdoor insectary until the subsequent emergence of the midges and parasites was completed.

This method of sampling is open to the criticism that in years when the galls are abundant it is probable that owing to the human factor large-sized galls would preponderate in the samples, whereas in years when the galls are scarce in order to reach the required number it would be necessary to pick galls of all sizes. This is a point to be considered because it is possible that the smaller sized galls may contain a higher proportion of parasitised midge larvae than the large-sized ones. On the other hand, the particular field in which the samples have been taken is always very heavily infested, practically every terminal and lateral shoot bearing a button, and it has never been difficult to collect sufficient numbers of galls. This high infestation is doubtless primarily due to the fact that the bolts of rods from all over these particular willow beds are brought into this field in which the pits are situated. Here the bolts are peeled and naturally an accumulation of midge larvae occurs; the heaps of

¹ Part of this sample was used for other purposes, leaving 488 galls for use in this study.

peelings near the pits also tend to increase the numbers of larvae present. No attempt has so far been made to destroy all these larvae, consequently when the adult midges emerge the nearest suitable place for oviposition is this field. From observation it is possible on occasion to see a diminution in intensity of attack as one proceeds from the end of the field which contains the pits towards the other end. Usually, however, this decrease only becomes obvious in the next field and further away from the first one.

When collecting the galls two rules have been observed: (1) care has been taken to reject any gall that has had its centre eaten out by birds, and (2) no choice has been exerted as to size of gall picked. Several persons have helped the writer in collecting the galls at different times. I am indebted to my wife, Mr A. Roebuck, and Mr H. C. F. Newton in this connection.

The samples of galls have been kept over winter in a lamp glass standing on muslin sewn on to an iron ring which is placed over a Petri dish containing water. A similar muslin-covered iron ring is placed over the top of the lamp glass. The water in the Petri dish evaporates through the samples of galls and so ensures the requisite degree of humidity. Occasionally (once a week in May, June and July) the top of the sample is sprayed with water in addition. This affects the numbers of midges emerging from day to day and temporarily sends up the emergence numbers. However, when weekly emergences are considered the effect is not appreciable.

Finally, the numbers of the midges and their parasites which have emerged have been noted daily, each day ending arbitrarily at 7 p.m. standard time (8 p.m. summer time).

III. IDENTIFICATION AND BIOLOGY.

The "button top" midge, *Rhabdophaga heterobia* H.Lw., is the best known of the gall midges which attack basket willows. The larvae cause galls known as "buttons" on the terminal shoots of many commercial varieties of *Salix triandra*, but recent work (3, 4) has shown that they cannot live on *S. viminalis*, *S. purpurea*, *S. viminalis* \times *purpurea*, *S. viminalis* \times *triandra* (Black Top) and *S. alba* var. *vitellina*. Later work has shown in addition that this species cannot live on *S. alba*, *S. caerulea*, *S. fragilis*, *S. nigricans*, *S. americana* and *S. repens*. Besides living in the buttons, the larvae also inhabit the male catkins and lateral buds.

Other midges with which it may be confused are *Rhabdophaga rosaria* H.Lw. and an unidentified midge whose larvae live in the terminal shoots of *Salix viminalis*, causing a dying off of the apex. The galls of *Rhabdophaga rosaria* are frequently to be found on wild *Salix* spp. of the broad-leaved type, and less often have been reported in commercial osier beds. The only attack so far observed by the author on commercially grown willows was on Cricket Bat willows (*S. caerulea*) being grown for sets in Norfolk. The midge and the gall are much larger than in the case of *Rhabdophaga heterobia*. The host plants

of *R. rosaria*, however, have not yet been critically examined. Magerstein (5) has recently dealt with a midge he has identified as *R. rosaria* and figures the galls on *Salix viminalis*, but in all probability he has misidentified the midge or else got several species confused.

A popular illustrated account of the bionomics of *Rhabdophaga heterobia* has recently been published (6), so that there is no need to rewrite it here.

In the field there appear to be two main broods a year, the adults of the over-wintering generation being on the wing from the end of April until the beginning of July and those of the summer brood being on the wing from July until September. In reality there is a succession of overlapping broods throughout the summer months, individuals of the last brood or broods remaining in the galls as fully fed larvae throughout the winter, unless they are scattered to the ground by birds pecking at the "buttons" or galls. Such individuals are able to survive in the soil and come to maturity.

While breeding this midge in an unheated open greenhouse at Rothamsted it has been the rule to obtain three flights of midges each summer; thus under these conditions there are three broods a year.

The time taken from when a newly emerged and mated midge commences to oviposit until the appearance of her first progeny in the adult stage has been studied in the summer broods. The average length of this period for the first brood in 1929 was 41 days with a percentage standard error of ± 3.93 ; that for the first brood in 1930 was 40 days with a percentage standard error of ± 1.65 . The average length of the same period for the second brood in 1929 was 35 days with a percentage standard error of ± 3.73 ; that for the second brood in 1930 was 44 days with a percentage standard error of ± 1.83 . The minimum time in both these broods and years was 33 days and the maximum 48 days. In all thirty-four experiments were involved. In 1933, in two experiments only, the time taken for the first brood was 38 days.

If we compare this unit of time for the first brood of 1929 with that of the second brood in 1929, using "Student's" *t* method¹, we arrive at the value 2.65 for *t*, which is significant. In the same way this unit of time for the first brood in 1930 can be compared with that of the second brood in 1930; similarly a comparison of the first brood in 1929 and the first brood in 1930 can be made, also between the second brood in 1929 and the second brood in 1930. The values for *t* in such comparisons are set forth in Table I.

Table I. Values for *t* for comparison of the shortest duration of life cycle in the summer broods of *Rhabdophaga heterobia* in 1929 and 1930.

Comparison	<i>t</i>	<i>P</i> =0.05
First 1929 brood with second 1929	2.65	2.45
First 1929 brood with second 1930	2.14	2.16
First 1929 brood with first 1930	0.82	2.11
Second 1929 brood with second 1930	5.78	2.16
First 1930 brood with second 1930	4.60	2.06
First 1930 brood with second 1929	2.98	2.11

¹ I am indebted to Mr F. J. Richards for assistance in this connection.

The result is that we find that the first brood in 1929 was significantly slower in reaching maturity than the second in 1929 and significantly quicker than the second in 1930. On the other hand, the first brood in 1929 reached maturity in about the same time as the first brood in 1930. Likewise the second brood in 1929 was quicker than that in 1930, the first in 1930 was quicker than the second in 1930 and the first in 1930 was slower than the second in 1929.

In this connection the temperature during these periods (May-June and July) is interesting and will be studied in more detail at a later date. The broods, mean quickest life cycle (i.e. the time taken from when a newly emerged and mated midge commences to oviposit until the appearance of her first progeny), and the excess or deficit of temperature compared with the average are set out in Table II.

Table II. *Duration of life cycle of Rhabdophaga heterobia compared with temperature.*

Brood	No. of exps.	Dates of oviposition and first emergence	Mean of quickest life cycle in days	Standard error	Excess or deficit in temp. ° F.	Average temp. (51-52 years)
First 1929	4	May 10-13 to June 20-25	40.75	±1.601	-1.4	54.5
First 1930	15	May 10-18 to June 19-28	39.53	±0.654	+1.7	54.5
Second 1929	4	June 24-26 to July 29-August 3	35.25	±1.315	+0.7	60.6
Second 1930	11	June 22-24 to August 2-10	44.27	±0.810	-1.6	60.6

All the midges of the same family do not emerge on the same day, and this duration of flight was found to vary from 4 to 29 days in different families. This variation does not necessarily depend on the number of individuals in the family, as can be seen from the examples shown in Table III.

Table III. *Duration of flight period and size of family.*

Family	No. of individuals	Duration of flight in days	Family	No. of individuals	Duration of flight in days
1	102	6	6	71	20
2	98	13	7	59	11
3	75	14	8	57	8
4	75	7	9	52	12
5	71	8	10	46	29

All the experiments were carried out under the same conditions as far as possible. The consequence of this variation in length of life cycles (since all the eggs are laid within 12 hours) between individuals of the same family is the overlapping of the generations.

An important feature in the bionomics of *R. heterobia* is that, although reproduction is sexual, unisexual families are the rule. Yet both sexes are normally to be found in a single gall owing to oviposition by more than one female. Thus random samples of galls produce populations which show normal sex ratios of 42-48: 58-52 (7).

The occurrence of hermaphrodite forms is interesting. Two such forms¹ have been seen in this species, one in 1928 and the other in 1933. Both individuals possessed normal female antennae and normal male genitalia. Altogether just over 19,000 *R. heterobia* have been examined. It is worth noting that when studying *Dasyneura alopecuri* (9) a similar occurrence was found once in 55,000 individuals, but in this case while the individual had normal male antennae it had an ovipositor. One other similar case in gall midges has been observed, i.e. in *Mayetiola phalaris* (10), and this individual had male antennae and an ovipositor. Unfortunately it has not been possible to recognise any of these specimens when alive.

The variation in numbers of antennal segments in *Rhabdophaga heterobia* has been studied (11) and found to depend on the food supply of the larvae.

IV. THE FAUNA OF THE GALLS.

The galls are ideal places for the hibernation of various insects and other animals, and the following is a list of what is considered to be typical of the hibernating fauna: Coleoptera—*Chalcoides* (*Crepidodera*) *chloris* Foudr., *Plectroscelis concinna* Marsh, *Coccinella 2-punctata* Linn.: Mollusca—*Helix nemoralis* or *hortensis* (young): woodlice—*Philoscia muscorum* (Scopoli): spiders—*Trachygnatha dentata* Wid., *Epeira cornuta* Clerk, *Oedothorax fuscus* Bl., and *Enidia bituberculata* Wid. All the above were found in galls collected in Somerset on November 23rd, 1927. I am indebted to Dr A. Randell Jackson and Mr H. C. F. Newton who identified the spiders and beetles respectively.

In addition, one frequently finds *Anthocoris nemorum*, which sucks the larvae in the galls and later the midges as they emerge. There are also aphid eggs, the predaceous larvae of a midge *Lestodiplosis* sp., which may be *L. heterobiae* Barnes, and the larvae of external parasites of *Rhabdophaga heterobia* such as those of *Pseudotorymus medicaginis* Mayr.

The following birds have been observed pecking at the button galls and presumably feeding on the insects contained therein—song thrush (*Turdus musicus* Linn.), blackbird (*Turdus merula*, Linn.), and various kinds of tits (*Parus* spp.). The latter probably scatter as much of the contents of the gall as they eat and so help to ensure the continuance of the midge, as the larvae can live and develop in the soil as well as in the gall itself.

V. SIZE OF POPULATION OF *RHABDOPHAGA HETEROBIA* AND ITS PARASITES, 1928–33.

The midge and its parasites have been reared each year from samples of 500 galls collected the previous October–November. Owing to the method of sampling no direct evidence of fluctuations in extent to which the crop has been attacked has been obtained. But the actual numbers of insects (midge and parasites) reared shows how the infestation might have varied. The average

¹ A third hermaphrodite was reared in 1934, in this case however the individual possessed normal male antennae and a normal ovipositor.

figures are expressed diagrammatically in Fig. 1. Table IV gives the numbers of midges and hymenopterous parasites reared from the standard sized samples over the period 1928-33. The figure for the year in each case denotes the year the insects emerged: the sample was collected the previous year.

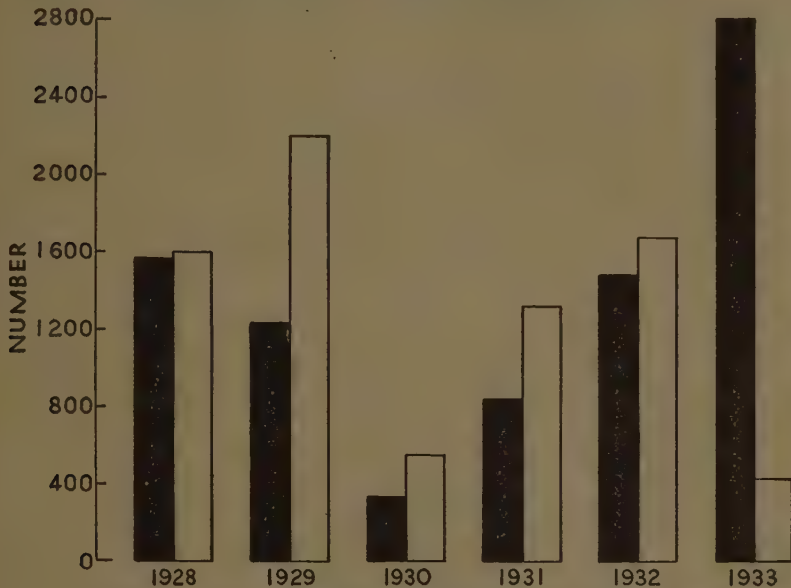


Fig. 1. Average numbers of *Rhabdophaga heterobia* (solid) and parasites (open) emerging from 500 galls, 1928-33.

Table IV. *Population of 500 galls of Rhabdophaga heterobia*, 1928-33.

Year	Total midges	Sex ratio	Total hymenopterous parasites	Parasitism %	Total insects
1928*	1573	42 : 58	1607	51	3180
1929	1235	43 : 57	2204	64	3439
1930 (i)	450	44 : 56	609	58	1059
(ii)	329	48 : 52	377	53	706
(iii)	244	45 : 55	682	74	926
1931 (i)	906	43 : 57	1470	61	2376
(ii)	867	42 : 58	1198	58	2065
(iii)	747	39 : 61	1302	64	2047
1932 (i)	1390	39 : 61	1632	54	3022
(ii)	1370	38 : 62	1589	54	2959
(iii)	1679	35 : 65	1766	51	3445
1933 (i)	2798	42 : 58	443	14	3241
(ii)	2633	47 : 53	350	12	2983
(iii)	3000	42 : 58	492	14	3492

* 488 galls comprised this sample, in all other cases 500 galls constituted a sample.

It will be seen at once that the total number of insects reared from the 500 gall samples was approximately 3000 in the years 1928, 1929, 1932 and

1933, but that in 1930 only about 1000 or one-third the usual number were reared and in 1931 only about 2000 or two-thirds the usual number appeared. The suggested reason for this reduction in total population is put forward below. However, it can be presumed that 3000 insects are the normal population obtainable from 500 galls. It is likely that this number is dependent on the food supply. Whereas in 1928, 1929 and 1932 the population was made up of roughly equal numbers of host midge and its parasites, in 1933 there was a large preponderance of midges and a corresponding decrease in numbers of parasites. Nearly twice as many midges as normal emerged, while just over one-quarter the usual number of parasites appeared. In spite of this striking change in make-up of the population, the total number was remarkably similar to that of 1928, 1929 and 1932. This sudden or cataclysmic reduction in numbers of parasites is further dealt with in section VI, "Relative parasitism of the midge."

The great reduction in numbers both of parasites and midges in 1930 and the consequent slow approach to normal as shown by the figures for 1931 are explicable as follows. In the summer of 1929 there was a serious drought and the willows stopped their terminal growth and started forming the winter buds, i.e. those which would remain over winter, considerably earlier than usual. Perhaps the descent of the sap had started much earlier than usual, and in any case the amount rising to the terminal shoots was seriously curtailed. The larvae of *R. heterobia* obtain their nourishment at the terminal buds and naturally the parasites depend on their host's food supply. It is reasonable to suppose that, owing to this shortage of sap, both the midge larvae and the parasites were short of food, and instead of each gall being able to support adequately roughly six insect larvae they could only support two the first year, i.e. 1929-30, and four the next year, 1930-1. It will be noticed that it took two years before the normal population (3000) was reached again; this means several broods, as only the over-wintering brood was studied.

As one collected the galls in 1929 the impression received was that they were smaller than usual though slightly less numerous. It was not until 1931 that they appeared as large as when collected in 1927 and 1928.

The effect of this drought on the plants was also very obvious. The willows in 1930 were badly stunted and only about one-third their normal height at the end of the year. The following year they were still much shorter than usual, roughly two-thirds their normal height, and in 1932 they were still slightly shorter than normal, but in this last case their abnormality was probably due in some part to the non-cultivation of the willow bed. In 1932 the owners ceased to look after the field, merely cutting the crop but not attempting to weed at all.

Another interesting observation is that the total numbers of midges per sample were increasing, the numbers of males appearing to be decreasing; e.g. in 1930, the year with the lowest midge population, the sex ratio varied from

44: 56 to 48: 52. As the numbers increased in 1931 the sex ratio varied from 39: 61 to 43: 57, and in 1932 when the midge population was apparently up to normal the sex ratio had decreased from 35: 65 to 39: 61. More data are required before this can be explained, as in 1933 the sex ratio was 42: 58 to 47: 53. However, it must be remembered that this species of midge produces unisexual families. It may be that in cases of overcrowding or any other deleterious factors the males are the first to suffer lethally. There is some evidence to support this, as previous work (8) on the effect of temperature on emergence showed that while females of another species of midge, *Dasyneura alopecuri*, were more affected by non-lethal factors, males were more affected by lethal ones.

VI. RELATIVE PARASITISM OF THE MIDGE.

(i) Identification.

I am indebted to Dr Ferrière of the Imperial Institute of Entomology for identifying some of the parasites for me. He reports finding the following in the tube of parasites which emerged in 1932: Chalcidoidea, Tetrastichini, *Aprostocetus ciliatus* Nees ♀ ♂ and *Tetrastichus inunctus* Nees ♀; Proctotrypoidea, Platygasterinae, *Synopeas gallicola* Kieff. ♀ ♂; and Torymidae, *Pseudotorymus medicaginis* Mayr ♀.

In addition to these, two further parasites have been reared in 1933, namely a *Platygaster* species and *Inostemma walkeri* Kieff. The latter, Dr Ferrière tells me, is that British species which Walker named *I. boscii*, but which is different from the real *boscii* Jur.

(ii) Methods and results.

The methods used were the same as those described in the first two papers in this series (1, 2).

The species of parasites reared have only been identified, and up to the present no attempt has been made to find out how prevalent each species has been from year to year. All the material has been kept for this purpose. In addition, before a true idea of the situation can be obtained, the interrelationships of the various parasites must be discovered.

However, the gross relative parasitism can be seen in Table IV, and the average yearly relative parasitism of the over-wintering brood is set out graphically in Fig. 2.

It can be seen that the relative parasitism has been more or less constant over the period studied, varying between 51 and 64 per cent., with the exception of 1933. This is in marked contrast to the comparatively large fluctuations obtained when studying the wheat blossom midges (1) and the meadow foxtail midge (2). But in these each successive brood of midges was being studied, whereas in this case the broods intervening between successive over-wintering ones have not been under observation. It appears possible that the relative

parasitism in these latter broods would reveal similar larger fluctuations, unless of course a stabilised condition between host midge and total number of parasites has been reached in this particular field of willows.

Since the fall in total numbers of insects in the samples in 1930 affected the numbers of midges and parasites to the same extent, the relative parasitism remained about the same. On the other hand, in 1933 there was a large de-

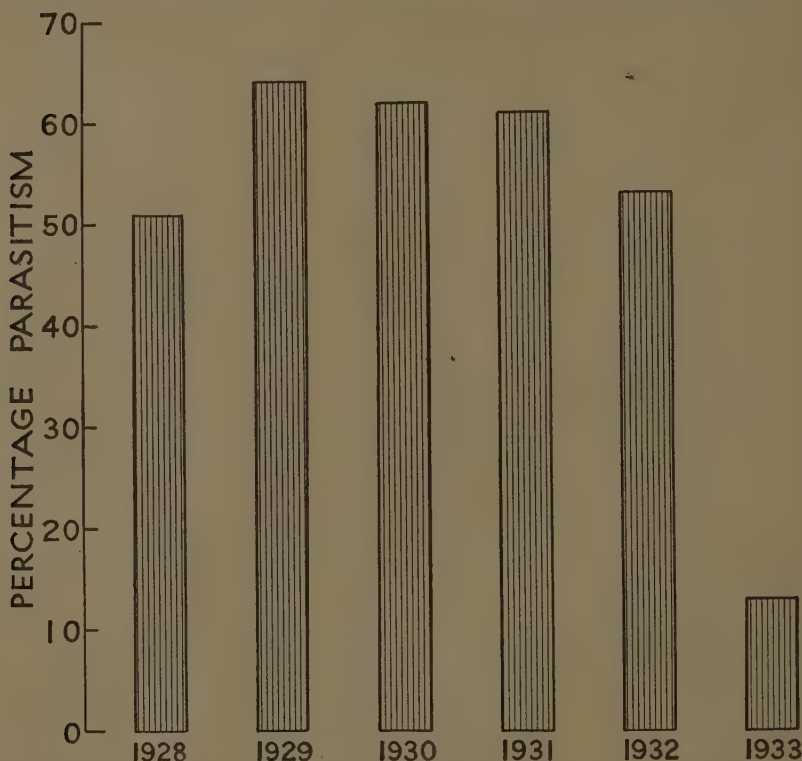
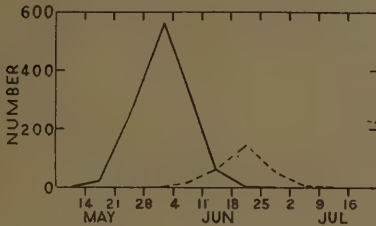


Fig. 2. Average relative parasitism of over-wintering brood of *Rhabdophaga heterobia*, 1928-33.

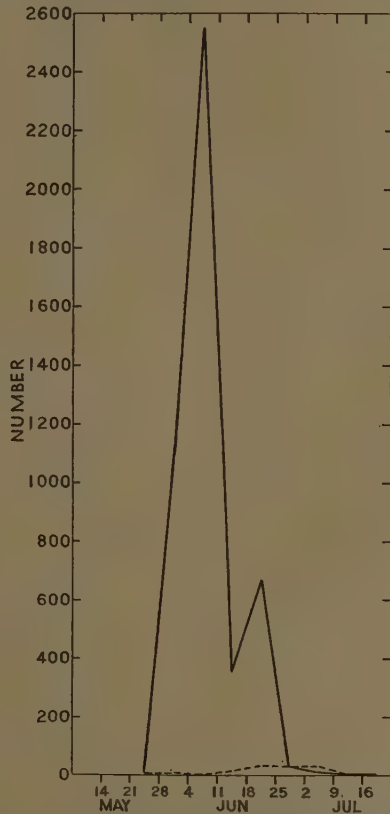
crease in the extent of the relative parasitism as the numbers of parasites emerging decreased and the numbers of midges increased. A reversal in the relative times of emergence of host and parasites, as has already (2) been suggested when dealing with another species of midge, *Dasyneura alopecuri*, is a possible explanation of this sudden fall in numbers of parasites. In Fig. 3 one set of normal emergence curves of *D. alopecuri* and its parasites are shown (A). In addition the abnormal emergence curves which represent the emergences occurring in 1928 are shown (B), together with the emergence

curves of the next brood which took place the subsequent year 1929 (C). It will be seen that normally the crest of emergence of the host midge is before

A. NORMAL EMERGENCE 1930
 TOTAL MIDGES 1244
 " PARASITES 284
 RELATIVE PARASITISM 19 PER CENT



C. RESULT OF ABNORMAL EMERGENCE 1929
 TOTAL MIDGES 4748
 " PARASITES 114
 RELATIVE PARASITISM 2.3 PER CENT



B. ABNORMAL EMERGENCE 1928
 TOTAL MIDGES 1588
 " PARASITES 979
 RELATIVE PARASITISM 38 PER CENT

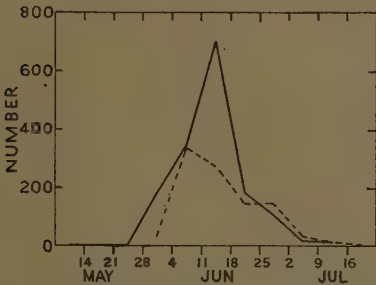


Fig. 3. Effect of alteration in relative times of emergence of *Dasyneura alopecuri* (full line) and its parasites (dotted line). A, normal emergence of *D. alopecuri* and its parasites; B, abnormal emergence, parasites relatively early; C, result of abnormal emergence, viz. increase of midges and fall in number of parasites in the following brood.

that of the parasites. In 1928, however, the peak of the parasites was ahead of that of the midges. As a probable direct consequence of this the numbers of midges increased from 1588 in 1928 to 4748 in 1929. Similarly the numbers of parasites fell from 979 in 1928 to 114 in 1929. The sudden fall in numbers

of parasites of *Rhabdophaga heterobia* in 1933 and the great increase in numbers of *R. heterobia* are possibly due to some such reversal in emergence dates of the previous generation. But since the over-wintering brood of this midge was the only one studied, we have no corroboration of this hypothesis.

VII. EMERGENCE.

Table V shows the dates of the actual first emergence, the peak of emergence, the number of days to reach the peak and the date of the last emergence of *R. heterobia* in the samples as kept in the outdoor insectary during the period 1928-33 inclusive.

Table V. *Dates of actual first emergence, peak of emergence, number of days to reach peak and the dates of the last emergence of Rhabdophaga heterobia, 1928-33.*

Year	Date of first emergence	Date of peak of emergence	Days to reach the peak	Date of last emergence
1928	April 29	May 28	30	July 9
1929	May 10	June 1	23	August 8
1930 (i)	" 10	" 2	24	July 24
(ii)	" 12	" 2	22	" 5
(iii)	" 14	" 2	20	" 2
1931 (i)	" 2	May 27	26	" 16
(ii)	" 6	" 27	22	" 16
(iii)	" 11	" 28	18	" 16
1932 (i)	" 17	June 13*	28	August 7
(ii)	" 18	" 13*	27	c. " 28
(iii)	" 16	" 13*	29	" 15
1933 (i)	April 26	May 29	34	c. July 17
(ii)	" 27	" 22	26	" 3
(iii)	" 25	" 22	28	" 11

* In each sample in 1932 there was a definite crest of emergence on June 2nd followed by a larger but abnormal crest on June 13th, a day after the weekly spraying for the year was started. It had been inadvertently omitted up to then owing to pressure of other work.

The range of first emergence is from April 25th to May 18th (23 days), while that of the peaks is from May 22nd to June 13th (22 days). Within samples of the same year the corresponding range between dates of first emergences has been 9 days in 1931, 4 in 1930, 2 in 1932 and 2 in 1933. In the case of the peaks it has been 1 day in 1931 and 7 days in 1933; in 1930 and 1932 the peaks occurred in the three samples on the same day. The time which lapses between the first emergence and the peak varies from 18 to 34 days if we consider the whole period of six years. The variation within any one year is much less, about one-half, e.g. 20-24 days in 1930, 18-26 days in 1931, 27-29 days in 1932 and 26-34 days in 1933.

Comparing these figures with those obtained when studying *Dasyneura alopecuri* (2), it will be seen that the dates obtained for the different samples of any one year agree more closely in the case of *Rhabdophaga heterobia* than in that of *Dasyneura alopecuri*. This difference between the two species may be due in part to the different over-wintering positions of the larvae. In the grass species, *D. alopecuri*, the larvae remain in the florets when they

Table VI. *Weekly emergence of Rhabdophaga heterobia and its parasites, 1928-33. The upper rows of figures refer to the midges, while the lower refer to the parasites. (Note. The true crest of emergence in 1932 was probably in the week May 28th-June 3rd.)*

Year	Date and size of sample	April 23-29	April 30-May 6	May 7-13	May 14-20	May 21-27	May 28-June 3	June 4-10	June 11-17	June 18-24	June 25-July 1	July 2-8	July 9-15	July 16-22	July-August later	Total parasites	Parasitism %
1928	1. xi. 27, 488 galls	1	33	102	84	330	590	236	156	31	8	1	1	—	—	1573	51
1929	31. x. 28, 500 galls	—	—	1	5	132	520	228	165	354	143	92	24	22	3	1607	64
1930	30. x. 29, 500 galls, A	—	—	3	41	115	216	60	7	3	1	2	1	52	13	2204	58
	B	—	—	1	31	40	128	151	335	58	38	12	2	1	—	609	53
	C	—	—	—	1	0	8	116	207	2	0	1	—	—	—	377	74
1931	31. x. 30, 500 galls, A	—	1	19	23	322	282	132	379	152	25	3	2	1	—	682	61
	B	—	2	9	18	310	416	117	507	159	40	54	79	41	19	1470	58
	C	—	—	5	13	215	79	340	397	101	48	50	87	62	17	1198	64
1932	30. x. 31, 500 galls, A	—	—	—	24	83	303	293	463	116	43	75	124	58	21	1302	54
	B	—	—	—	4	2	26	137	505	117	35	10	3	0	17	1390	54
	C	—	—	—	30	71	279	200	521	491	371	70	52	5	17	1632	54
1933	1. xi. 32, 500 galls, A	6	80	198	485	935	902	151	35	570	342	71	67	18	5	1679	51
	B	4	34	138	439	1034	114	472	49	36	2	1	0	1	0	2798	14
	C	5	38	146	467	1120	715	234	33	0	1	1	3	5	0	443	12
					2	30	95	101	53	33	16	14	7	0	0	2633	14
					467	669	478	33	3	4	6	1	1	0	0	350	
					1	42	104	57	57	62	36	36	12	4	1	3000	
																492	

fall to the ground and so will find themselves in all kinds of exposed and unexposed positions, under leaves, etc. But in the other species, *Rhabdophaga heterobia*, the larvae remain in the buttons or galls on the tips of the willow shoots and so are all exposed to the same conditions, i.e. atmospheric conditions as opposed to varying soil surface conditions as is the case in *Dasyneura alopecuri*.

It is hoped to study the factors controlling day to day emergences in detail at some later date.

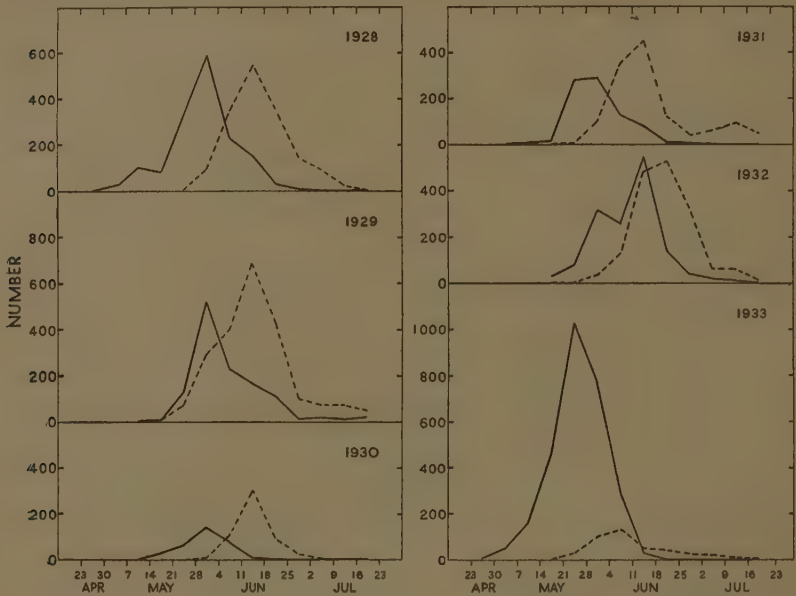


Fig. 4. Weekly emergence of *Rhabdophaga heterobia* (full line) and its parasites (dotted line), 1928-33.

The dates and figures in Table VI show the weekly emergences of the midge and its parasites. The top row of figures in each case refers to the midge, while the lower row refers to the parasites. The peaks are in heavy type. It will be seen that a weekly crest of emergence has occurred five times in the week May 21st to 27th, five times in the week May 28th to June 3rd, once in the week June 4th to 10th, and three times in the week June 11th to 17th. But in contrast to what happened in the case of *D. alopecuri* (2) there is little difference between the samples of any one year.

The emergence of the parasites has varied less, the crest occurring in the week June 4th to 10th three times (1 year), in the week June 11th to 17th eight times (4 years), and in the following week, June 18th to 24th three times

(1 year). No variation occurred in the samples of any one year. Usually the crest of emergence of the parasites occurs in the second or third week after that of the host midge.

Fig. 4 shows the average weekly emergence numbers of the midge and its parasites over the period 1928-33. The figures have been obtained by averaging the three samples of each year. The constancy of the date of the weekly crest of emergence of the midges and the parasites is very noticeable.

The emergence of both the midge and the parasites drags out a long while. This may be so in the field, it may not. Under insectary conditions of keeping water evaporating through the sample and spraying the top of it once a week, one obtains definite minor peaks occurring the day after such spraying. Table VII shows this.

Table VII. *Showing effect of spraying top of sample weekly during the emergence period. Evening of spraying marked with asterisk.*

Date (June)	No. of midges emerging		No. of parasites emerging	Date (June)	No. of midges emerging		No. of parasites emerging
	♂	♀			♂	♀	
3*	53	45	61	14	8	1	30
4	20	35	55	15	7	9	107
5	2	4	13	16*	3	2	58
6	0	3	25	17	34	44	221
7	17	32	81	18	15	14	115
8	11	14	26	19	10	10	93
9*	7	21	98	20	8	6	71
10	35	37	104	21	2	0	36
11	11	7	95	22	0	1	13
12	4	3	39	23*	0	4	47
13	7	15	139	24	26	17	56

This indicates how beneficial a shower of rain might be in the field.

It has been shown previously (8) that considerable emergences may take place at intervals during May if the weather is favourable, but do not under adverse weather conditions. It was then stated that extra cold given to the larvae during the winter tended to retard the initial emergence, and so causes the crest of emergence to be reached sooner. Also that cold affected the larvae of *Dasyneura alopecuri* less than those of *Rhabdophaga heterobia*.

These facts, together with the appearance of minor crests after the main crest, lend colour to a view that is being built up and strengthened by these studies of gall midges. This view is that the larvae require a certain more or less fixed amount of temperature to develop from fully fed larvae into adults; when such amount of temperature has been made available to the insects, then under given favourable conditions from day to day emergences will take place. On the other hand, however, favourable day to day conditions may occur before such amount of requisite temperature has been received, emergences will not occur. The actual day to day emergences seem to depend upon day to day conditions to some extent, but finally, when the insect is ready, the urge to emerge is overwhelming and as a result the crest of emergence is

nearly constant. Attempts are being made to obtain a rough index figure for this necessary amount of temperature without studying the threshold developmental temperatures for each stage. If such an index can be obtained one of the objects of this investigation will have been achieved.

VIII. SUMMARY.

1. This is the third of a series of studies on the fluctuations of insect populations in the field and is concerned with the gall midge *Rhabdophaga heterobia* H.Lw.

2. The time taken by this midge to complete a life cycle is discussed, and notes are given of occurrences of hermaphrodite individuals in gall midges.

3. A list is given of various spiders, beetles and other animals which have been found hibernating in the galls of this midge.

4. The changes in populations of the midge and its parasites in the overwintering generation have been traced over a period of six years, 1928-33. A drought which seriously damaged the growth of the willows is claimed to have caused a great diminution in numbers of both host midge and its parasites. It is pointed out that the numbers did not re-attain the normal until the third year after the drought.

5. The relative parasitism of the midge for this period of six years is given. A sudden fall in the relative parasitism in 1933 is discussed and compared with a similar occurrence noted in the second of this series of studies.

6. The emergence of the midge and its parasites is set forth. It is shown that the date of the peak of emergence of the midge is nearly constant whether the initial emergences are earlier or later than normal.

IX. ACKNOWLEDGMENTS.

I am indebted to the persons mentioned in the context for their help in diverse directions and also to Dr C. B. Williams and Dr A. D. Imms for discussing various points with me. I wish to acknowledge my thanks to Mr A. D. Dunkley who has again prepared the figures.

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A GENERAL ACCOUNT OF THE PESTS ON WILLOWS AT SYSTON, LEICESTERSHIRE

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(With Plate VIII and one Figure in the Text.)

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I. LOCATION, ETC.

THE Syston willow beds are situated about four miles north of the city of Leicester. They are bounded on the south by the road from Syston to Wanlip. on the west by the River Soar and on the north and east by grass fields. The total area is 75 acres. It is divided by dykes, and in some cases hedges also, into nine fields indicated by letters on Fig. 1.

All but the "Eight-acres" (A), on the extreme south of the beds, have been growing willows for over 40 years. Field A contains about 8 acres of willows and half an acre, around the gate in the south-east corner (X), is devoted to the processing of the rods. It contains sheds, pitting dykes, and space for sorting, peeling, couching, etc. This field was planted in 1918. It was previously under grass. It was double-ploughed; one plough skimmed off the grass and turned it into a deep furrow, the second plough, working deeply, placed the soil on top of the grass. In this soil the rods were planted.

The subsequent history of the field has shown that this preparation was inadequate, and grass has been the most persistent weed.



Fig. 1. Diagram of the Syston willow beds.



Phot. 1. View from the bridge looking north. Field A on the right.

Every winter the beds are horse-hoed. This has to be done in sections when they are free from flood water. Field A missed this treatment in the winter 1931-2.

Hand-hoeing is continued when the shoots are growing.

Manuring with artificials has never been uniform, but plots have been dressed from time to time. Complete fertilisers have given good results, that is, an increased length of rods. Nitrogen dressings, either as nitrate of soda or sulphate of ammonia, have produced equally good results. Potash in the form of kainit, sulphate of potash, or muriate of potash has also materially increased growth.

Phosphate has been applied in the form of superphosphate, but apparently produced a scab which penetrated to the rods, causing a "specking."

II. VARIETIES OF WILLOWS.

The following varieties are grown, the letters in brackets referring to the fields on the plan. *Salix triandra* varieties: Black Maul (all fields), Whissender (G, H), Newkind (K), Hollander (K), Spaniard (H), French (E, H), German (K), Black Top (K), a hybrid *viminalis* × *triandra*; *Salix viminalis* varieties: Merrin (G), Continental (D, G, H); and *Salix purpurea*, a few Dicky Meadow (F). Fields A, B and C were wholly planted with Black Maul. Field C was grubbed up in 1931. Dr Barnes's data on *Rhabdophaga heterobia* have been obtained on Field A.

III. INSECTS.

The insect fauna of these beds is very extensive, both as regards species and individuals. Two factors of supreme importance should be noted in connection with insect attacks on the willows. One is the predilection of a species of insect for a species of willows: *Phyllodecta vulgatissima* will eat only *Salix viminalis* and *Rhabdophaga heterobia* only *Salix triandra*, etc. The second is the fact that natural phenomena, meteorological factors, etc., far outweigh other methods of combating the pests, such as parasitism or direct control measures. The following are the species of outstanding importance.

The aphids *Melanoxantharium salicis* L. and *Aphis saliceti* Kalt., especially the former, occur fairly regularly on *Salix triandra* and *S. purpurea*. They are effectively controlled by nicotine dusts.

The blue willow beetle (*Phyllodecta vulgatissima* L.). The earlier history is not known, but by 1920 this pest was present in immense numbers, defoliating the *Salix viminalis* varieties. In spite of sundry sprayings and sweep traps during the next few years there was little indication of any change in its numbers. On June 3rd, 1922, as many as 206 beetles were counted on a single shoot about 8 in. long, and the average would be between 50 and 60 per shoot. It should be noted that experimental data showed that persistence

in spraying could have controlled them, especially in the adult stage, although the cost may have seemed high.

Floods, from which the beds have suffered increasingly during the last decade, undoubtedly washed many of the hibernating adults down the river. From experimental data on the drowning of the larvae, or disease following prolonged submersion, the writer believes the wet June of 1927 virtually exterminated the pest. It was in that year that the numbers suddenly and greatly declined. The wet July of 1930 completed their destruction, and it is now difficult to find a single specimen on the beds.

The drab or brown willow beetle (*Galerucella lineola* F.) attacks only the *Salix triandra* varieties, skeletonising the leaves. It appears rather later than *Phyllodecta* and the larvae are most abundant in July. It first appeared as a pest in 1921 and continued until 1930. There was a severe attack in progress during July 1930, threatening complete defoliation of about 30 acres of Black Maul. Rain started on July 13th and, with two breaks of two days, continued to July 30th. By July 23rd practically all the larvae were dead. Only a few now remain.

Pontania proxima Lepel. causes the familiar red bean-like galls on *Salix triandra*. It was exceptionally bad in 1926 and 1930, and considerably reduced the lengths of the rods. It is impossible, yet, to say what factors are influencing its numbers. In 1926 60 per cent. of the leaf surface was covered with the galls, whereas in 1933 it was difficult to find odd specimens of the first brood.

The button-top midge (*Rhabdophaga heterobia* H.Lw.), which attacks *Salix triandra* varieties, was present on the older portion of the willow beds and at once became established on the "Eight-acres" on which Dr Barnes has made his studies. Various proprietary washes and nicotine dusts were applied in the early season when the midges were emerging, but they did not appear to influence the numbers in succeeding generations. Since 1926 practically every rod on Field A, and a high proportion of rods on the rest of the beds, have been attacked by this midge by the end of each year. Further notes on this species are given under "Preparing the rods."

Rhabdophaga marginemtorquens Winn. curls the edges of the leaves of *Salix viminalis* and in some years may produce an appreciable diminution in the length of the rods.

Certain species of gall midges (*Rhabdophaga* spp.) produce clean-cut holes in the bark and mine the rods. They are only found on the 2- and 3-year-old plants, chiefly the varieties Black Maul, German and Newkind. The secondary effects of these are more harmful than the insects themselves. Birds, either suspecting the presence of insects or actually finding them emerging, peck round the holes and strip the bark. In this way the rods are further damaged.

IV. BIRDS.

The principal nesting birds number 18. They are chiefly insectivorous and play a not inconsiderable part in controlling certain of the insects. The larger ones, lapwing (*Vanellus vanellus*), snipe (*Capella gallinago*) and moorhen (*Gallinula chloropus*), probably play no part in controlling the smaller insects on the rods. The wood pigeon (*Columba palumbus*) probably only uses the hedges for nesting. The following are summer migrants: whinchat (*Saxicola rubetra*), whitethroat (*Sylvia communis*), willow warbler (*Phylloscopus trochilus*), sedge warbler (*Acrocephalus schaenobaenus*) and reed warbler (*A. scirpaceus*). The following are resident throughout the year: thrush (*Turdus philomelus*), blackbird (*T. merula*), great tit (*Parus major*), coal tit (*P. ater*), marsh tit (*P. palustris*), blue tit (*P. coeruleus*) and reed bunting (*Emberiza schoeniclus*).

The migrants and residents feed on the caterpillars, Diptera, etc., and have so far prevented any outbreaks by a number of species. None of them feed on the beetle adults or larvae (*Phyllodecta* or *Galerucella*). The migrants have no effect on *Rhabdophaga heterobia*, but the residents split open the "buttons" in the autumn and winter, eating some of the larvae and scattering others on the ground.

V. FLOODING.

Great trouble has been experienced by the growers through flooding. It is firmly believed that in recent years floods have been worse, both more frequent and more prolonged. Both the River Soar and its principal tributary the River Wreak have long been known to flood during wet periods, especially in winter. These rivers meet just a little north of the beds, consequently a sudden rise by either river causes water to overflow the lower beds on the north side of the block. From the ordnance survey maps there appears to be only a difference in height of 4 ft. between the highest ground on Field A and the lowest on the north side. The river beds are not systematically cleaned and weeds have grown in recent years, tending to hold up further any flowing silt. Owing to the rapid growth of the city of Leicester in recent years, there is a feeling that the flow from the sewers has much increased, further adding to the risk of floods by holding back the flow of the Soar alongside the willow beds. In addition, during the period reviewed by Dr Barnes, there has been only one hard winter, 1928-9. There is less risk of flooding in a hard winter, because so much of the precipitation is held up as snow or ice on the land, and this may be gradually taken away by the river in its normal channel.

VI. PREPARING THE RODS FOR USE.

Cutting the rods begins after the leaves have fallen, and lasts from the end of October to the beginning of December. As far as possible the lower lying beds to the north are cut first. The rods are brought to the area X in Field A for sorting into lengths. The graded ones are then carted away to the

factory for "buffing." All the "rough" is stacked on the ground until wanted for "brown."

During the sorting, numbers of *Rhabdophaga heterobia* larvae fall on this piece of ground from the shaken "buttons." Rods cut from the end of December to May are "pitted" for "white." After sorting they are put into bundles and stacked upright in the pitting dykes until required for peeling from May to July, commencing after the sap is flowing freely. Rods cut after May are peeled after sorting without having to be pitted. A variety such as Newkind is "couched" first on this same ground.

It will be seen that, on this portion around the pitting dykes adjacent to Field A, *Rhabdophaga heterobia* larvae receive ample protection. This is the highest ground and therefore least liable to be flooded. The larvae on the ground are less likely to be drowned or washed away downstream. In addition the "buttons" project safely from the pitting dykes until after the emergence of the midges. For specially long rods, blocks are left for two or three years before being cut. These blocks also act as foci of infection.

It is very noticeable in some years, such as 1929 and 1930, how infection with this midge spreads from the pitting dykes and from uncut blocks of willows, until by the end of the season the attack is uniform over the beds. The writer believes that the floods destroy all those on the ground, and if only all the *Salix triandra* varieties could be cut and carted away for preparation, one good flood winter would rid the beds of this pest.

THE WINTER STARLING ROOSTS OF GREAT BRITAIN, 1932-1933

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(With four Maps in the Text.)

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I. INTRODUCTION.

FOR hundreds of years the habit of the starling (*Sturnus vulgaris* Linn.) of collecting into vast flocks to roost during the winter months has been well known. There are many excellent descriptions of the way in which the flocks converge to some reed bed or small wood from a very large area, and of the remarkable aerial evolutions in which they often engage before settling down for the night. Apart from these general accounts, there have been several papers dealing with the subject in greater detail; the most important of these are the survey of the roosts in Shropshire carried out by Forrest (5) in 1900, and Wynne-Edward's (15 and 16) papers on the Devonshire roosts in 1928-9.

The object of the present investigation was to locate as many as possible of the major starling roosts in Great Britain which were in use during the period October 1932 to April 1933, and to collect information of all kinds about them. The method employed was to send out printed questionnaires and to appeal to observers all over the country to send in reports. This was done by means of appeals in the press, and, through the kindness of the British Broadcasting Corporation, on the wireless. Whenever possible the help of a reliable observer was obtained to oversee the returns dealing with each county.

In response to these appeals, many hundreds of reports were received from all parts of the country, giving varying amounts of information. In many cases there were several reports about one roost, and so they could be checked

against one another. Amongst those which could not be checked there are doubtless instances of faulty and incomplete observation, but when all the information is combined for the whole country it is felt that a reasonably accurate picture of the general conditions is obtained. A big starling roost is a conspicuous thing, and it is unlikely that very many have been missed.

In addition to the position of the roost, information was asked for on other points, such as the age of the roost, the kind of cover used, the effect on the trees, and so on. Here again, though such reports may often be inaccurate, it is felt that the general conclusions drawn from a large number of them will be worth consideration, and they are dealt with below.

The starling has increased very much in numbers during the past hundred years, in some parts of the country at least. Early last century it was rare in many districts, especially in winter, but in the eighteenth century and earlier it seems to have been quite common. It is clearly desirable to obtain some idea of the present status of a bird which is increasing and which appears to have undergone considerable fluctuations in numbers in the past, particularly in view of its possible effect on agriculture. It is impossible to estimate the number of starlings in a roost with any accuracy, even in favourable cases, and so the only way to attack the problem is to study the number and distribution of the roosts themselves, having a rough idea of their size. This is the aim of the present investigation, and it is hoped that it may be of use as a basis for comparison with similar work in the future. No previous survey on a national scale has been carried out, and so there is very little information with which to compare the present results. Only roosts estimated to contain 500 birds and upwards are included in this survey¹.

II. DISTRIBUTION OF ROOSTS.

From the whole of Great Britain reports of 285 roosts occupied during the winter 1932-3 have been received. As roosts are often occupied for a short time during the autumn and then abandoned for a more sheltered situation, it was hoped to compile a list of the roosts occupied in January 1933, January being a month when there is little movement of roosts taking place. However, it proved to be impossible to obtain the necessary information for all the roosts, and so the total number occupied at any time between October 1932 and April 1933 is considered. This number will include the same group of birds more than once if they changed their roost during the winter, but this point is ignored as the exact number of cases is not known, and it is felt that the slight excess thus produced will tend to counterbalance roosts which have been missed altogether.

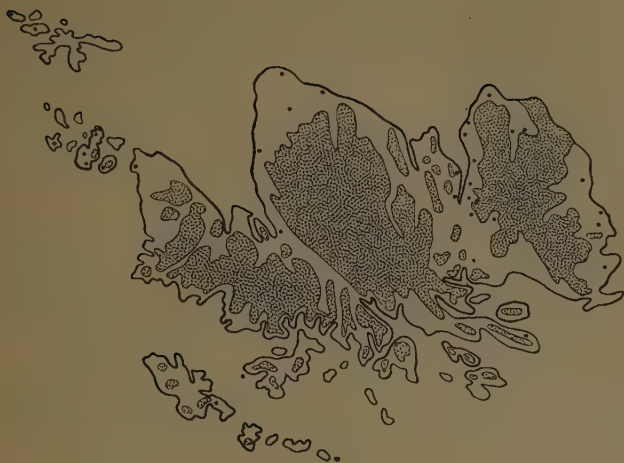
Of these 285 roosts, 224 were in England, 39 in Scotland, and 22 in Wales. Maps 1 and 2 show the approximate positions of the roosts and also the distribution of land over 600 ft. above sea-level. (For details see Tables V

¹ The detailed records are being deposited in the files of the British Trust for Ornithology at Oxford.



Map 1.

Map 1. Showing the approximate positions of the roosts in England and Wales. Land over 600 ft. stippled.



Map 2.

Map 2. Showing the approximate positions of the roosts in Scotland. Land over 600 ft. stippled.

and VI at the end of this paper.) It will be noticed that with very few exceptions the roosts lie in areas below 600 ft. The notable exceptions are two roosts in Central Wales, one of which is near the Usk Valley where the birds feed, and three in West Yorkshire. One of these, a small roost of two or three thousand birds, at Queensbury near Bradford, at a height of 1200 ft., is the highest one recorded. This distribution may be accounted for by the fact that starlings habitually feed in pasture land and are seldom met with above the limit of cultivation, while the flocks flying to roost have a curious tendency to avoid passing over hills (3, 10).

In calculating the density of roosts in each county the number per thousand square miles was taken, so as to express the result as a whole number. Counties were used for convenience in dealing with the reports, though they are unsatisfactory units of area in some respects (Map 3). As most of the roosts are below 600 ft. and the feeding area is practically confined to the lower land, the area below 600 ft. in each county was measured and the density of roosts expressed per 1000 square miles of this. Map 4 shows the densities after this elimination of the high land has been made.

Two counties were without roosts, Rutland and Middlesex. They are so small that the feeding areas of neighbouring roosts could easily cover them. The longest authenticated flight line from feeding grounds to roost is 30 miles. Radnor and Caernarvon, which are among the counties with the greatest density, are both mountainous, and so the density on the lower parts is very high. Radnor had only one roost and only 37 square miles below 600 ft., and therefore appears amongst the densest counties.

Considering the general distribution, it is dense in the counties south of a line joining the Severn and the Wash, with the exceptions of Norfolk and Suffolk, especially in the central part of the area. Then a less dense region stretches from the Wash to the Severn, and the north-western midlands are again thickly populated. The east coast counties are all thinly populated, only three out of the nine exceeding four roosts per 1000 square miles. In Wales most of the roosts are in the less mountainous region of the south, but in the north there are a few in the low land near the coast. Central Wales is devoid of roosts altogether (Map 1).

It does not seem possible to correlate this distribution with any of the features of the country. As one would expect, the south, and south-east and north-west midlands have most roosts, but the less dense strip across the middle is unexpected. This follows roughly the outcrop of the liassic strata, but it is improbable that this has any significance, as elsewhere, in Wiltshire and Dorset, this formation has more numerous roosts. The scarcity along the east coast might possibly be due to more frosty conditions in winter or to the large areas of land under corn.

In Scotland there are doubtless a good many roosts unrecorded, especially along the west coast where small ones are found in the cliffs. Map 2, showing



Map 3.

Map 3. Showing the density of roosts per 1000 square miles of total area in the different counties.



Map 4.

Map 4. Showing the density of roosts per 1000 square miles of land below 600 ft. in the different counties.

the positions of the Scottish roosts, brings out well the way in which they occur in the low-lying coastal districts. Several also occur in the Orkneys and Shetlands, usually in the cliffs.

From old records it seems that starlings were rather rare birds about a hundred years ago, except in the Shetlands, Orkneys, and islands on the west of Scotland and Ireland. Before that they were apparently much commoner, and in 1564 a reward for their heads was instituted. They increased during the last century, especially from about 1885 onwards, and spread westward as a breeding species into Devon and Cornwall (4), Scotland (6), and Ireland. At the present time they are residents in all districts, and the distribution of the roosts suggests that they have more or less completely populated the country. They do not appear to be increasing now as they were twenty or thirty years ago, and of twenty estimates of change which I have received, twelve report a decrease in numbers.

Forrest (5), in his survey of the Shropshire roosts in 1900, recorded twenty-one, most of which had been occupied for many years. He stated that the big roosts were mostly deserted after the middle of November, and the birds either migrated, returned to the towns, or went about in small parties roosting in the nearest convenient place. Some other records of about the same date also mention this desertion of the roosts in late autumn. It seems possible therefore that a change has taken place, and the roosts are now occupied all winter instead of being abandoned in the autumn. There is also a certain amount of evidence (3, 5) that the present roosts are larger and more widely spaced, but the material for comparison on these points is unfortunately small.

III. ROOSTS IN TOWNS.

A large number of starlings roost in the centre of London, often on buildings, but roosts in other towns are not very common. There was a large roost on Dublin Cathedral, and others on a clock tower in Belfast, on buildings in Glasgow and in shrubberies in Edinburgh, Manchester, and in a few other places. Roosting on buildings is extensively practised by starlings in American cities.

The task of recording roosts in London is difficult owing to the number of small and ephemeral roosts. Some twenty are reported from Greater London, varying in size from about 7000 birds to about twenty, the estimated total starling population being about 15,000—20,000 birds. Only three small roosts are in the region south of the river, and those on the north are mostly right in the town. Ten of these roosts are on buildings, including the largest, which is on St Paul's and has an estimated population of 7000 birds. The feeding area of the northern group is in the north and western directions within a radius of roughly 10 miles, and accounts of vast flocks of starlings converging on London from miles around are much exaggerated.

According to Macpherson (9) the roosts in London were originally in trees in the parks and squares, but that as the birds became more numerous they took to the buildings. The roost on the Nelson Column was in existence in 1910. At the present time the birds roost in the trees in Trafalgar Square until the leaves fall, when they move on to the National Gallery, and St Martin's-in-the-Fields. A previous survey of the London roosts was carried out by E. M. Nicholson in the winter of 1925-6 with very similar results to this present one, except for a possible decrease in the number of birds.

IV. "AGE" AND SITES OF ROOSTS.

As would be expected there is a great deal of variation in the number of years that a starling roost is in use, but in the majority of cases they are reoccupied year after year for many years. Reports were received as to the age of 247 roosts, and of these 107 have been in use for over ten years, and eighty-four for less than ten and more than two years. The roost on Lundy Island, which fluctuates in population from a few dozen birds up to many thousands according to the weather on the mainland, is known to have existed with only short breaks for 180 years. Another very old roost is in the reeds of Slapton Ley, South Devon, known for 135 years, while of roosts of forty years and upwards nineteen are recorded. On the other hand, eighteen roosts were first occupied in the winter of 1932-3.

If the starlings have settled in a suitable cover and are not disturbed, they normally continue to roost there for many years, probably as long as the place remains suitable for them. Sometimes most or all of the birds will desert one of these roosts for a year or more, but as a rule it will be reoccupied again. Several roosts are reported to have had a very long break between two periods of occupation; for example, the roost at Bisterne, Hampshire, was occupied forty years ago and then not till 1925 onwards.

It is impossible in most cases to decide why the starlings have selected a roosting site, as they may fly miles to it past places apparently identical. They seem to be very strongly influenced by habit in returning to a roost, and will do so even if forcibly driven out. In the case of these reoccupied roosts it can hardly be the memory of the birds which brings them back after so many years, but probably only chance.

Besides these long-standing roosts, a smaller number of them are much more transitory in nature. These are often due to the persecution which the birds undergo from the landowners, so that they are never allowed to settle down in one place for long. In this way a roost may move from one cover to another, all within a mile or two of each other. Severe gales sometimes cause the birds to find new roosting sites so as to avoid a long flight to and from the feeding ground, and these new roosts may continue in use afterwards. A few instances are recorded of large roosts appearing for one winter only and then disappearing from the district altogether. An example of this

occurred at Retford in 1929. Here hundreds of thousands of starlings roosted in a small wood from August to the end of December and then apparently left the neighbourhood altogether. Such movements may perhaps be due to disturbance of some other roost, or possibly to the movements produced by weather conditions.

From the figures given above it appears that at least three-quarters of the roosts in the country have been occupied for more than one season, and of these a large proportion are used year after year and may be regarded as stable.

As soon as the breeding season is over, and the young can fly, starlings begin to assemble in flocks for feeding and roosting purposes. These summer and early autumn roosts are often not used all through the winter, but, usually in October or November, the birds move into another roost where they may remain until the next breeding season. This desertion of the roost in the autumn often takes place in the case of roosts in reeds, probably owing to the reeds dying and breaking down. In this way one gets "linked" roosts, a reed roost occupied in summer and autumn and a roost in a wood to which the birds move when deserting the other. Several cases of this have been reported. (The same kind of thing often takes place with roosts in deciduous trees, perhaps due to the exposure after the leaves have fallen.) In a few cases the autumn roost is occupied until the end of December and then abandoned.

Information concerning the period of the year during which the roosts were occupied was not always available. It is also a subject on which reliable information is difficult to get owing to the necessity of visiting the roost many times during the winter. The reports on 205 roosts are given in Table I. The

Table I. *Periods of the year roosts are occupied.*

Summer to October	39
Summer to January	6
October to January	15
January to April	14
All winter	117
All year	14
	<hr/> 205

dates are only approximate, as the times of the changes from one roost to another are very variable both between different roosts and in the same one in successive seasons. An attempt was made to determine the effect of the type of cover in the roost on the period of occupation. Information was only available for ninety-nine roosts, but Table II shows the tendency for reed

Table II. *Periods of the year in which the different types of roosts are occupied.*

	Summer to October	October to January	January to April	All winter
Reeds	8	2	—	10
Deciduous trees	10	4	—	9
Evergreens	1	1	1	16
Conifers	1	3	4	22
Thorns	—	—	1	6

and deciduous roosts to be deserted while evergreen ones are occupied all winter. Non-breeding starlings remain in flocks using a roost during the breeding season, and so certain roosts are occupied all the year round.

The favourite situation for a starling roost is a reed bed or small dense plantation. The actual type of cover seems to be immaterial as long as it is dense, but the roosts used all through the winter are mostly in conifers, rhododendrons, or laurels. The birds appear to prefer to be crowded together and will roost so thickly on the reeds that they break them down. If roosting in a fairly large wood they usually remain mostly in one part and do not scatter themselves through it.

Table III. *Different types of cover used for roosting.*

Reeds	52	Thorns	19
Conifers	48	Buildings	12
Deciduous	47	Cliffs	8
Evergreens	37	Oil condensers	5

Besides ordinary roosts of this kind there are several unusual situations. In the Orkneys, Shetlands and Hebrides, roosts are found in caves and cliffs along the coasts, owing to the scarcity of trees. On an island off the Irish coast a few starlings are recorded as roosting on the ground in tunnels in the rough grass (8). A very peculiar situation for a roost was at Peterhead, on a large floating crane which was stranded there, and a more exposed situation could hardly be imagined. Starlings still roost on the cranes in the dockyard at Peterhead, and also at Dublin and Belfast. Another unusual site for a roost is afforded by the oil works in West Lothian. Here the starlings roost between the pipes of the oil condensers, which are always warm. The warmth may be the attraction, as at one works, when the condensers were allowed to go cold, the starlings left. Five roosts of this kind have been reported, and in each case many thousands of birds are present.

V. EFFECT OF A ROOST ON THE TREES AND VEGETATION.

When several hundred thousand starlings roost in a small wood every night for five or six months, their droppings accumulate and produce various effects. In some roosts it is reported that there is a layer of droppings as much as 8 in. thick on the ground, and that the trees are so thickly covered that they appear to be whitewashed. This thick covering of guano may have a serious effect on the trees. A number of reports have been received on this subject, and in most cases it is spruce and Douglas firs which are affected. On an estate in North Devon starlings began to roost in a covert of larch, spruce and Douglas fir, in the autumn of 1922. When thinning was carried out in 1925 two-thirds of the trees were dead and the rest sickly. The firs suffered most, the larch least (1). In another case in Cumberland a plantation

of ten-year-old spruce was killed in six months. Pine trees may survive longer than spruce, and besides these, rhododendrons, hazel, larch, elder, bamboo, holly and ivy are reported as being killed, also the vegetation growing under the trees.

This effect on the trees probably only occurs when the roost is very large and the birds crowded together into a small space. They are even said in some places to roost so thickly that their weight breaks down the branches. In the great majority of roosts the birds seem to have little or no effect on the trees, and laurels are benefited and flourish in a roost. One correspondent stated that the underwood was stimulated, but the quality of the wood was impaired and lost its toughness, so that hurdles made from it soon showed signs of wear.

Apart from the effect of the droppings on the trees there is the question of the presence of seeds which have passed unharmed through the alimentary canal of the bird. One of the most characteristic features of an old roost is a thick undergrowth of elders, whose fruit is one of which starlings are very fond. In the roost near Retford, already mentioned, which was only occupied for four months, a dense growth of elders resulted. There must be large numbers of plants introduced into the roost in this way, as fifty-seven plants of six species have been raised from the droppings of thirty-eight starlings (11). During the present investigation reports of thick growths of dead nettles, large red poppies, gooseberries, black-currants, chickweed, nettles, and various grasses have been received.

The quantities of guano accumulating in a large roost have sometimes been removed and tried as a garden fertiliser. Some correspondents report that it is useless, being too strong, but others state that it is good when diluted with ordinary soil. It is never likely to be of any great value owing to the difficulty of collecting it.

VI. EFFECT OF A ROOST ON OTHER BIRDS, AND ON ANIMALS.

The foul conditions in a starling roost are often said to drive out other birds and animals, and in some cases movement of a roost from one cover to another has been attributed to the foulness of the wood being too bad for the starlings themselves. The question on the schedule about other birds which used the same roost produced reports on ninety roosts, the information being shown in Table IV. From this it appears that though the presence of starlings may have some deterrent effect on other birds, it by no means drives them all away, as some accounts suggest. The other birds do not as a rule roost actually with the starlings but tend to occupy the less crowded parts. In some cases there may be actual hostility. Wynne-Edwards has described (16) the eviction of redwings from their roost by starlings which occupied it, but this does not seem to have often been observed.

It is often stated that pheasants are driven out of a wood if starlings come to roost there. Four reports have been received of this, but in twelve the pheasants were unaffected by the presence of the starlings. On one estate in Devon the covert in which the roost was situated was used for rearing pheasants, and some 200 of them roosted there as well as the starlings.

Table IV. *Other birds using the same roost as the starlings.*

No other birds	24	Redwings and fieldfares	7
Finches and small birds	18	Rooks	5
Pigeons	18	Magpies and jays	3
Blackbirds and thrushes	15	Wagtails	2
Pheasants	12	Woodcock	1
Sparrows	10	Gulls	1

In the same way it is said that foxes are driven from a roost and the covert rendered useless for hunting. This may not always be due to the fact that foxes are absent, as in one case, after the hounds had drawn a roost without success, a fox was seen to come out, its scent apparently masked by that of the starlings' droppings.

The large flocks of starlings assembling to roost, form an easy food supply for predatory birds. Hawks have often been observed taking a bird from the flocks, sometimes many evenings in succession. I have had reports of thirty-six cases of sparrowhawks seen at the roosts, and in four they were actually seen attacking the starlings. In one case they lived near but did not molest the flocks. On an estate in Devon, where sparrowhawks had been exterminated altogether by the keepers, eleven were shot in twenty-five days after a starling roost was established there.

Eighteen examples of kestrels seen at a roost have been reported, but many of these appeared infrequently or were clearly not concerned with the roost. In one case a kestrel was seen attacking the starlings, in another one it seemed to be frightened of the flocks, and in a third the kestrel was said to eat dead starlings but not to kill them. The peregrine is reported seven times and the buzzard five, on two of which occasions it was seen attacking the starlings. Owls also attack them, and I have disturbed a tawny owl during the day from within the roost itself.

At Hastings the starlings were driven from the roost by "two large black birds, possibly carrion crows." This is very curious, if the birds were really responsible for the desertion of the roost, as there seem to be no similar cases recorded. The nearest occurred at the Manchester roost when the starlings did not enter the roost as usual for some time, and when they did a hawk came out. Occasionally the starlings will mob a hawk, three cases being recorded.

Very little is known of the relation of mammals to the starling roosts. Rats are often common, and the disjointed remains of starlings often seen under the trees are probably due to them. Starlings often die in the roost and

the rats doubtless eat their dead bodies. I had a report of foxes barking and jumping up at the birds in the trees, and another of an otter eating a starling near the roost.

Seigne (13), writing of a starling roost in Ireland, states that hawks kept away, and a cat was seen chased and buffeted by a flock. He also describes an attempted invasion of the roost by another flock which resulted in a series of battles in the air and on the ground. After one of these, over 100 dead were counted. He mentions two other cases, one of which took place over Cork in 1929 and lasted for hours. Again numbers of dead and wounded birds were picked up. I know of no other records of fights between starling flocks.

VII. DIRECTION OF APPROACH, ETC.

In order to test a suggestion that most of the flocks came to roost from the east side, observers were asked to send in information on this point. Out of 190 cases the numbers from the different points of the compass are almost equal, and though there is a slight excess from the east, this is so small that it can have no significance.

The greatest distance between roost and feeding ground which has been accurately determined is 30 miles, recorded in South Devon. Distances of 12-20 miles are quite common, so that one roost may have a very widely extended feeding area. In some cases flocks will cross estuaries or arms of the sea in going to the roost. They cross the Sound of Stromness, the Forth, the Solent and the Bristol Channel, and flocks have been seen leaving the Scilly Isles for the mainland.

VIII. THE STARLING AND AGRICULTURE.

The accusations usually directed against starlings are that they pull up and destroy sprouting wheat and that they eat a great deal of fruit. Several of my correspondents, both farmers and fruit-growers, denied this, so it may not be a universal habit.

Collinge in 1927 gives the constitution of the food as containing 20.5 per cent. of cereals, 15.5 per cent. of cultivated fruit, 33.0 per cent. of injurious insects and slugs, and 7 per cent. of weed seeds and wild fruits. He concludes that they are beneficial from April to June, neutral during the next three months and harmful during the other six months. This is a more harmful estimate than the Ministry of Agriculture Report (14). This concluded, from an examination of 748 birds, that they ate nearly five times as many harmful as beneficial insects, and that any quantity of grain was only eaten during October, November, and December. Even during these months more injurious insects than corn are usually eaten.

There is no doubt that a considerable amount of corn is eaten by starlings during the autumn. On the other hand, the damage they do is probably

counteracted by the number of injurious insects they destroy. In the present state of knowledge of their food relations, it would be most unwise to interfere seriously with their numbers.

In 1890 the starling was introduced into America at New York. Since then it has spread and increased so that it has colonised most of the eastern part of the United States. Its food has been carefully studied in that country (7) and found to be beneficial or neutral to man. It does attack fruit to a certain extent, and also maize, but very little wheat. In the monthly average of its food, grain forms only 1·16 per cent. and cultivated fruit 4·41 per cent. of the whole. When the numbers increase to saturation, as in this country, it is probable that more corn and fruit will be eaten, and if our starlings become still more numerous the damage done will probably increase. From what has been said above it seems that the great rate of increase of thirty or forty years ago has fallen off very much now, and the situation as regards agriculture does not demand drastic measures to be taken.

IX. SHIFTING A ROOST.

Owing to its possible effect on a covert, not only from the point of view of the trees themselves, but also because of hunting and game preserving, and the unpleasant smell, should it be near a house, a starling roost is usually regarded with disfavour by landowners. Many attempts have been made to drive the birds away, and this often proves to be a very difficult task. The birds are very reluctant as a rule to abandon a roost and, if driven out, often move only a short distance, and not infrequently into a place even less desirable than the first.

Various methods have been employed to disturb the birds, and it is often necessary to continue for several nights in succession. Shooting is most often tried, and succeeded in fourteen cases out of thirty-one reported to me. It may be very expensive, as at one place a fortnight's shooting with twelve guns failed, and at another £30 worth of cartridges and fireworks only drove them away for a few days. Other methods of disturbance, such as bonfires, lamps hung in the branches, and smoke from dead leaves, have been tried with varying success. A more drastic method is to burn sulphur so as to drive the birds out with the fumes. This seems to have the desired effect, but is seldom tried for fear of killing the trees. Several methods of fumigation are given in the *U.S. Bureau of Agriculture Bulletin* (7). More interesting is the report of a successful eviction by flying a hawk-shaped kite over the roost. I have also heard of an inconclusive attempt with box-kites, and one with balloons which were said to be successful "while they lasted." It seems curious that the starlings should fear a kite when the presence of a hawk at a roost is so common, and a more extensive trial of this method would be interesting.

X. SUMMARY.

1. An account is given of an attempt to locate all the major starling roosts in Great Britain during the winter 1932-3.

2. 285 roosts were located and their distribution discussed. Almost all are below the 600 ft. contour line.

3. The effect of roosting starlings on the trees, on other birds, on predatory animals, and in scattering the seeds of plants is considered.

4. A brief account of past changes in numbers of starlings is given and their relation to agriculture based on various analyses of food is discussed. As their rate of increase is less it does not appear that any drastic thinning of their numbers is necessary at present.

5. The starling roosts of Greater London are considered apart from the rest. About twenty roosts are recorded with an estimated total population of 15,000-20,000 birds.

6. Mention is made of various methods employed in driving starlings away from a roost.

XI. ACKNOWLEDGMENTS.

An investigation of this kind is only possible with the co-operation of a large number of observers, and I wish to express my thanks to the several hundred helpers who have sent me information during the course of the work. In particular I am indebted to the British Broadcasting Corporation for the opportunity of broadcasting an appeal on the National transmitter, and for subsequent publicity, and also to the editors of numerous newspapers who have published my letters. I also wish to thank the following societies and observers for their invaluable help in dealing with counties and other large areas throughout the country: the Cambridge Bird Club, the London Natural History Society, the Midlothian Ornithological Club, the Oxford Ornithological Society, Miss D. Steinthal, and Messrs F. C. Blathwaite, P. Bywaters, S. Cramp, R. Groome, P. H. T. Hartley, A. C. Jones, G. Marples, E. M. Nicholson, M. E. W. North, H. Morrey Salmon, A. P. Scott, V. D. van Someren, G. M. Spooner, M. I. Stancliffe, C. W. Walker. Mr A. H. Machell Cox not only dealt with the roosts of Devon and Cornwall but kindly allowed me access to the great mass of material he has collected during many years of work on this subject, an account of which it is to be hoped he will eventually publish. Reports on the Cambridgeshire (12) and Cheshire (2) roosts have already been published.

Finally, I wish to record my indebtedness to my wife for constant help throughout the whole of the work.

Table V. *The number of roosts in each county and their density per 1000 square miles.*

County	No. of roosts	Density per 1000 sq. miles	Density per 1000 sq. miles under 600 ft.	County	No. of roosts	Density per 1000 sq. miles	Density per 1000 sq. miles under 600 ft.
Anglesey	1	3.6	3.6	Lancashire	9	4.8	6.0
Bedford	5	10.6	10.6	Leicester	5	4.8	5.0
Berkshire	6	9.6	10.4	Lincolnshire	8	3.0	3.0
Brecon	1	1.3	9.1	Merioneth	1	1.5	5.0
Buckingham	5	6.7	7.3	Monmouth	1	1.8	2.5
Cambridge	8	9.3	9.3	Montgomery	1	1.2	3.5
Cardigan	1	1.4	3.1	Norfolk	6	2.9	2.9
Carmarthen	2	2.2	3.8	Northampton	3	3.0	3.0
Carnarvon	3	5.2	10.4	Northumberland	5	2.5	4.5
Cheshire	10	9.7	10.3	Nottingham	1	1.2	1.2
Cornwall	13	8.3	11.1	Oxford	5	6.7	7.1
Cumberland	2	1.3	2.2	Pembroke	4	6.5	7.9
Denbigh	1	1.5	4.2	Radnor	1	2.1	27.0
Derbyshire	2	2.0	4.3	Shropshire	8	5.9	7.7
Devon	11	4.3	5.7	Somerset	9	5.6	6.7
Dorset	5	5.1	5.5	Stafford	8	6.9	9.0
Durham	3	3.0	4.6	Suffolk	3	1.4	1.4
Essex	5	3.3	3.3	Surrey	5	5.5	6.1
Flint	1	3.9	5.2	Sussex	11	8.5	9.0
Glamorgan	5	6.3	9.0	Warwick	2	2.1	2.1
Gloucester	3	2.4	3.0	Westmorland	1	1.3	3.2
Hampshire	10	7.5	7.7	Wiltshire	5	3.7	4.3
Hereford	4	5.0	5.7	Worcester	3	4.2	4.4
Hertfordshire	6	9.5	9.5	North Yorkshire	4	1.9	2.9
Huntingdon	1	2.7	2.7	East Yorkshire	3	2.6	2.7
Isle of Wight	2	13.6	13.6	West Yorkshire	12	4.3	7.0
Kent	6	3.9	4.1				

Table VI. *Winter starling roosts, 1932-3, in Great Britain.*

England and Wales.

Anglesey.
 Maelog Lake.
Bedford.
 Apsley Guise.
 4½ miles south-east of Bedford.
 3 miles south-west of Bedford.
 Between Hitchin and Biggleswade.
 Guilden Morden.
Berkshire.
 Twyford.
 Wantage.
 Windsor.
 Burchett Green.
 Fyfield.
 Winkfield.
Brecon.
 Llangorse Lake.
Buckinghamshire.
 North Marston.
 Great Missenden.
 Dadford.
 Chearsley Furze.
 Stoke Goldington.

Cambridge.
 Littleport.
 Elsworth.
 Great Chishall.
 Longstowe.
 Wicken.
 Burwell.
 Reach.
 Great Wilbraham.
Cardigan.
 Cardigan.
Carmarthen.
 Carmarthen.
 Whiteland.
Carnarvon.
 Aberdaron.
 Afonwen.
 Great Orme.
Cheshire.
 Aldford.
 Waverton.
 Stretton.
 Disley.
 Farndon.
 Birkenhead.
 Staleybridge.

Cheshire (contd).
 Blakenen.
 Combermere Park.
 Dunham Park.
Cornwall.
 Bodmin.
 Land's End.
 Falmouth.
 Lamellen, near Wadebridge.
 Egloskerry, 4 miles west of Launceston.
 Quethiock, east of Liskeard.
 Eglosdale, Wadebridge.
 Kilkhampton, south of Hartland.
 Tywardreath, north-east of Par Station.
 Trewithen, near Truro.
 Perranwell Station.
 Launceston.
 Carnanton.
Cumberland.
 Gosforth.
 Siddick.
Denbigh.
 Vale of Clewyd.

Table VI (continued).

<i>Derbyshire.</i> North Wingfield. Foremark Hall.	<i>Huntingdon.</i> Fenstanton.	<i>Nottingham.</i> 8 miles north-east of Nottingham.
<i>Devon.</i> Petrockstow. Slapton Ley. Afferton. Gittisham. Filleigh. Sowton, near Exeter. Bucks Cross, Clovelly. Tuell Down. Tavistock. Holne Park, River Dart. Bere Alston.	<i>Isle of Wight.</i> Niton. Northwood Park, Cowes.	<i>Oxford.</i> Blenheim. Fritwell Gorse. Fullbrook. Wychwood Forest. Henley Park.
<i>Dorset.</i> Sherborne. Abbotsbury. Burton Bradstock. Iwerneminster Estate. Oakley.	<i>Kent.</i> Blean. Denton. Tonbridge. Snodland. Shorne. Canterbury.	<i>Pembroke.</i> Upton Bottoms. Kingsbridge. Fishguard. Skokholm.
<i>Durham.</i> South Shields. Bishopton. Tunstall.	<i>Lancashire.</i> Ellel Grange. Morecambe. Rainford. Childwall. Rossall. Wavertree Park, Liverpool. Aigburth. Blackpool. Platt Fields, Manchester.	<i>Radnor.</i> Gladestrey.
<i>Essex.</i> Southend. Langham. Newport. Margaretting. Witham.	<i>Leicester.</i> Leicester. Woodthorpe, Loughborough. 8 miles west of Market Harborough. Bushby. Coalville.	<i>Shropshire.</i> Whitchurch. Walcot. Valeswood. Hodnet. 2 miles north of Craven Arms. Lymore. Near Ellesmere. Ludlow.
<i>Flint.</i> Prestatyn.	<i>Lincoln.</i> Skegness. 19 miles north of Lincoln. 2½ miles south-east of Navenby. Harmston. Reeds Island, Humber. Dumholme. Boston. Burton Coggles, Grantham.	<i>Somerset.</i> West Moor Parish. Halse, Taunton. Charleton Mackrell. Yeovil. Bridgewater. 5 miles from Clevedon. Flax Bourton. Broomfield. Castle Cary.
<i>Glamorgan.</i> Oxwich. Swansea. St Fagans. Barry Island. Rhymery Viaduct.	<i>Merioneth.</i> Aberdovey.	<i>Stafford.</i> Keele Hall. Wednesbury. 2 miles north-east of Stafford. Walsall. 3 miles west of Uttoxeter. Lichfield. West Bromwich. 7 miles west of Dudley.
<i>Gloucester.</i> Nailsworth. Badminton. Sherborne.	<i>Monmouth.</i> Tredegar Estate, Newport.	<i>Stafford.</i> Keele Hall. Wednesbury. 2 miles north-east of Stafford. Walsall. 3 miles west of Uttoxeter. Lichfield. West Bromwich. 7 miles west of Dudley.
<i>Hampshire.</i> Bisterne. Near Liss. Romsey. Compton Manor. Fullerton Hall. Mouth of Hamble River. Near Aldershot. Faccombe.	<i>Montgomery.</i> Llanymynech.	<i>Stafford.</i> Keele Hall. Wednesbury. 2 miles north-east of Stafford. Walsall. 3 miles west of Uttoxeter. Lichfield. West Bromwich. 7 miles west of Dudley.
<i>Hereford.</i> Shobdon Park. Holme Lacy House. Haugh Wood. Arkstone Wood.	<i>Norfolk.</i> Weybourne. Ormesby Broad. Hickling Broad. Belton. Weasenham. Litcham High House Farm.	<i>Stafford.</i> Keele Hall. Wednesbury. 2 miles north-east of Stafford. Walsall. 3 miles west of Uttoxeter. Lichfield. West Bromwich. 7 miles west of Dudley.
<i>Hertford.</i> Letchworth. Caddesden. Royston. Tring. Brocket. Bishop's Stortford.	<i>Northamptonshire.</i> Orton Longueville. Woodford. Great Walton, 8 miles north-east of Kettering.	<i>Suffolk.</i> Lowestoft. Haverhill. Near Wrentham.
	<i>Northumberland.</i> Colt Crag Wood. Dudley. Gosforth Park. Belford Hall. Seahouses.	<i>Surrey.</i> Coptthorne. Merstham. East Horsley. Cheam. Ockley.
		<i>Sussex.</i> Battle. Buckhurst Park. Clapham Wood. Falmer. Hastings. Haywards Heath.

Table VI (*continued*).

<i>Sussex</i> (contd).	<i>Wills.</i> (contd).	<i>Yorkshire</i> (contd).
Lower Dicker.	Near Salisbury.	Barnsley.
Wiston.	Blundsdon Abbey.	Brompton (East Riding).
Loders Gorse.	Knighton Wood.	Dearne Gorse.
Boxgrove.		Kippax.
Winchelsea.	<i>Worcester.</i>	Bradford.
<i>Warwick.</i>	Forthampton.	Near Leeds.
Stratford.	Stourbridge.	Pontefract.
Ethington.	Pershore.	Hebden Bridge.
<i>Westmorland.</i>	<i>Yorkshire.</i>	Spofforth.
Askham.	Skipton.	Redcar.
<i>Wiltshire.</i>	Brompton (North Riding).	Lund.
Castle Combe.	Penistone.	North Dalton.
Marden.	Whiston Grange.	Queensbury.
	Melton.	Thirsk.
Scotland.		
<i>Aberdeen.</i>	<i>Inverness.</i>	<i>Lothian</i> (contd).
Tifty.	Lentram.	Tranent.
Peterhead.	Darwins.	Winchburgh.
Craigiebuckler.		
<i>Argyll.</i>	<i>Kincardine.</i>	<i>Moray.</i>
Campbeltown.	Felterlain.	Kingston.
<i>Berwick.</i>	<i>Kirkcudbright.</i>	<i>Orkney.</i>
Ayton.	Newton Stewart.	Near Stromness.
<i>Caithness.</i>	<i>Lanark.</i>	Brough.
Brough.	Power Station, Glasgow.	Deersound.
<i>Dumfries.</i>	Carluke.	Hoy.
Lochmarten.	<i>Lothian.</i>	Westray.
Whiteloch, Colvend.	Edinburgh.	Stromness.
5 miles north of Dumfries.	Kelso.	
<i>Fife.</i>	Broxburn.	<i>Shetland.</i>
Dumferline.	West Barns.	North of Unst.
Aberdour.	North Berwick.	Northmavine.
<i>Harris.</i>	Livingstone, Mid Calder.	Haroldswick Bay.
Tarbert.	5 miles east of Melrose.	Mid Yell Voe.
		Haseosay.

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THE MOSQUITOES OF NAMANVE SWAMP, UGANDA

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WITH AN APPENDIX ON THE ESTIMATION OF ORGANIC
CARBON IN WATERS

By G. GRIFFITH.

(With Plates IX-XI.)

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I. INTRODUCTION.

NAMANVE swamp, which lies on the northern shores of Lake Victoria and was at one time an arm of this lake, is a large papyrus swamp, 6-7 miles long and with a minimum width of half a mile. It is in progress of afforestation with *Eucalyptus*, and fringed with natural forest except where this has recently been felled. A main ditch has been dug throughout its length and a few



Photo. W. J. Eggleston

Phot. 1. The main ditch running through the earlier planted portion of the papyrus swamp (habitat type 7).

secondary ditches transversely; these have considerably lowered the original water-level in most parts of the swamp, but their effect was not greatly in evidence when the work on which this paper is based was begun.

A general account of the swamp is given by Eggeling (1934), and a more detailed account by the same author (1935); he divides the vegetational types of Namanve as follows: (i) The Lily Zone, (ii) Fringing Papyrus, (iii) Fern and Sedge, (iv) *Limnophyton* Swamp, (v) Papyrus Swamp, (vi) *Miscanthidium* Swamp, (vii) *Phoenix* Swamp.

My observations have been confined almost entirely to the last three zones, as this investigation was primarily economic and intended to ascertain the effects of draining and planting on the Anopheline fauna. The first four types of vegetation occur in conditions where drainage and planting are out of the question and where collecting has to be made from a canoe; for this reason their fauna is only very briefly considered. Records of mosquitoes from swampy forests, which are intermediate between rain forest and *Phoenix* swamp, have been added for the sake of completeness.

II. METHODS.

Collections were made weekly from March 15th, 1932, to March 29th, 1933, in selected pools in the various plant communities, the pools being numbered and indicated by stakes as shown in Pl. X, phot. 2 and Pl. XI, phot. 4. The number and species of mosquito larvae obtained by dipping ten times with an enamel pie-dish were recorded for each pool, and the average numbers of larvae collected per pool in each habitat are given in Table I¹. Certain species of mosquito larvae cannot be obtained by this method; these include the whole genus *Mansonia*, of which the larvae obtain the required air by piercing the roots or submerged stems of plants. The mosquitoes associated with *Pistia* were not studied in this swamp, but are discussed by Mr G. H. E. Hopkins in a forthcoming monograph on Ethiopian mosquitoes to be published by the British Museum. The collections were made as far as possible by the same native collector to avoid errors due to slight individual variations in the method of dipping, and the writer checked the work when possible. In a few cases, where a pool was nearly dry, it was not possible to obtain more than a ladle-full of water, but the error from this cause is small and has been allowed for as far as possible. The numbers of larvae recorded in Table I are somewhat less than those actually collected: some losses occur when mounting material for examination and, during the earlier part of the work, some of the less common species were removed for isolation and died; predaceous larvae such as *Culex* (*Lutzia*) *tigripes* sometimes devour larvae in the tubes. While it is impossible for Table I to be entirely free from errors, the numbers of larvae collected have been sufficiently large in most cases to give a very fair picture of the preferences of the various species for the different

¹ The complete figures for samples have been deposited for reference at the Imperial Institute of Entomology in London.

types of pool; where the numbers are small they have been included in the table, though it is possible that in a few cases the record may be due to an error in labelling or in entering up of identifications.

III. THE MOSQUITO FAUNA.

(a) *Types of pool.*

The types of pool selected were as follows:

(1) Main drainage ditch where it passed through slashed *Phoenix* swamp. Two pools.

(2) Main drainage ditch passing through planted, slashed and virgin papyrus and *Miscanthidium* swamp. Five pools.

(3) Slashed *Phoenix* swamp. Four pools.

(4) *Phoenix* swamp. Four pools.

(5) Cut *Miscanthidium* swamp. Three groups of two, four and three pools respectively (the last three pools are tabulated as B in Table I).

(6) Recently burned papyrus. Three pools.

(7) Papyrus, burned earlier. Six pools.

(8) Virgin papyrus. Four pools.

(9) Virgin *Miscanthidium*. Four pools.

Trees had been planted in the areas covered by types (5), (6) and (7), but in type (6) the planting was practically coincident with the beginning of the observations.

The period covered by the observations was slightly more than a year, March 1932–April 1933, except in the case of the *Phoenix* swamp and virgin *Miscanthidium* where observations were begun two or three weeks later.

(b) *The main drainage ditch (types 1 and 2).*

This ditch extends throughout the length of the swamp, and is about 3–4 ft. deep and 6 ft. wide. The edges are kept cleared but a little grass often overhangs the water, and trailing floating grasses, *Ricciocarpus* and filamentous algae can sometimes be found at the edges. The water in this ditch is for the most part peaty, but in the two pools included in type (1) there is a large admixture of surface water, which drains into the swamp, and this contains a considerable amount of suspended clay. After heavy rain the milky appearance, indicating surface water, may be seen for a considerable distance down the drain. From Table I it can be seen that, while *Anopheles coustani*¹ occurs equally in both types, *A. gambiae*² prefers the surface water. In type (2), sixteen *A. gambiae* occurred in pool No. 2 and fifteen in pool No. 4; these pools were not far distant from the pools of type (1). In pools No. 8 and No. 9, which were about a mile farther down the swamp, only one and two specimens respectively were collected; pool No. 16 was entirely negative for this species as were two further pools (not included in the table) which

¹ Better known as *A. mauritanus*.

² Better known as *A. costalis*.

Table I. Average number of larvae of mosquitoes collected per pool in each habitat.

	Main drain in papyrus and swamps	Main drain in papyrus and swamps	Pools in slashed <i>Phoenix</i> swamp (type 1)	Pools in slashed <i>Phoenix</i> swamp (type 3)	Pools in <i>Phoenix</i> swamp (type 4)	Pools in <i>Miscanthidium</i> (type 5A) (type 5B)	Pools in recently burnt papyrus swamp (type 6)	Pools in papyrus swamp burnt earlier (type 7)	Pools in virgin papyrus (type 8)	Pools in virgin <i>Miscanthidium</i> (type 9)
	209.5	56.5	188.6	16.2	6.7	43.1	167.0	1.0	13.0	2.2
<i>Anopheles constani</i> Lav.	—	—	6.8	—	—	11.7	—	—	—	—
<i>A. gambiae</i> Giles	—	—	—	1.2	1.2	—	—	—	—	—
<i>A. implexus</i> Theo.	—	—	—	0.7	—	—	—	3.7	—	—
<i>Aedes albopictus</i> Theo.	—	—	—	5.0	—	—	—	2.7	—	—
<i>A. domesticus</i> Theo.	—	—	—	18.0	3.7	—	—	72.7	—	4.7
<i>A. lineatopennis</i> Ludl.	—	—	—	0.7	0.2	—	—	1.3	—	3.2
<i>A. mucidus</i> Karsch. (1)	—	—	—	—	2.7	—	—	—	—	—
<i>A. punctithoracis</i> Theo.	—	—	—	—	0.2	—	—	—	—	—
<i>A. tarsalis</i> Newst.	—	—	—	17.4	9.2	—	—	1.3	—	24.0
<i>Culex annulirostris</i> Theo. } (2)	—	—	101.6	?	0.2	18.7	51.3	1.7	1.0	—
<i>C. aurantipes</i> Edw.	—	—	—	—	—	0.1	—	0.2	—	—
<i>C. decens</i> Theo.	—	—	—	—	—	1.0	—	—	—	—
<i>C. duttoni</i> Theo.	—	—	—	—	—	6.0	26.7	0.2	—	—
<i>C. guarti</i> Blanch.	—	—	24.8	—	—	—	—	—	—	—
<i>C. kingianus</i> Edw. (3)	—	—	—	5.0	8.9	—	—	—	—	0.2
<i>C. pallidoccephalus</i> Theo.	—	—	—	—	—	1.8	0.7	—	—	5.7
<i>C. pipiens</i> L.	—	—	—	—	—	0.1	—	—	—	2.7
<i>C. poecillipes</i> Theo.	—	—	—	—	—	—	—	—	—	—
<i>C. rubinotus</i> Theo.	—	—	—	9.5	15.7	6.8	—	3.7	7.2	3.0
<i>C. senibrunneus</i> Edw.	—	—	—	0.2	—	—	—	—	—	—
<i>C. theileri</i> Theo. (4)	—	—	—	—	—	—	—	0.2	—	—
<i>C. tigripes</i> Grp. (1)	—	—	0.2	—	—	5.2	—	—	0.5	—
<i>C. univittatus</i> Theo.	—	—	9.4	7.2	1.7	240.0	7.3	57.5	6.2	2.7
<i>Ficobia hispida</i> Theo (5)	—	—	—	—	—	—	0.3	0.3	0.2	—
<i>F. mediotineata</i> Theo.	—	—	—	—	—	3.3	—	—	—	—
<i>F. mimomyiaformis</i> Newst.	—	—	—	—	—	0.1	—	—	—	—
<i>F. plumosa</i> Theo.	—	—	0.2	—	—	—	—	—	—	—
<i>F. uniformis</i> Theo.	—	—	—	—	—	3.7	—	—	—	—
<i>Hodgesia saugunea</i> Theo.	—	—	—	—	—	4.0	—	—	12.0	5.5
<i>Uranotaenia alboabdominalis</i> Theo.	—	—	—	—	0.2	—	—	—	4.2	2.0
<i>U. balfouri</i> Theo.	—	—	—	8.0	4.5	0.2	—	—	2.5	19.7
<i>U. hopkinsi</i> Edw.	—	—	—	—	—	—	—	—	—	0.2
<i>U. mashaensis</i> Theo.	—	—	—	—	—	—	—	0.2	2.2	1.5
<i>U. pallidoccephala</i> Theo.	—	—	—	—	0.5	—	—	—	4.5	?
<i>Uranotaenia</i> spp.	—	—	—	—	—	0.7	—	—	—	0.7
<i>Corethrella</i> sp.	—	—	—	—	—	0.5	—	—	—	2.7

(1) Predaceous.

(2) The larvae of these two species are apparently inseparable, so the species are placed together. In the text they are referred to as *Culex annulirostris*. Ecologically there is little apparent difference in the requirements of the larvae, but *C. aurantipes* appears to prefer somewhat more peaty water (British Museum monograph).(3) One *Culex antiremus* was bred from a similar batch of larvae. As the larvae of this latter species is unknown it is possible that further specimens are included under *kingianus*.

(4) Identified from larva only, no adults obtained.

(5) Larvae of the type described by Macfie and Ingram (*Bull. Ent. Res.* 7, 1916, p. 14).

were established in November 1932 in a still more remote part of the ditch where no milky appearance had ever been observed. The Culicine faunas of types (1) and (2) are also markedly different, type (2) being rich in *Culex annulioris*, *C. guiariti* and *C. univittatus*, whereas in type (1) only a few *C. guiariti* were found.

The water in this ditch is exposed to full sunlight, and on a bright day the time required for the paper in a Watkins' exposure meter to take up the requisite tint was only $2\frac{1}{2}$ sec.; under the shade of the banks the time taken was 20 sec. Some shade is given to larvae from the fringing or floating vegetation.

The temperature of the surface of the water in which the mosquito larvae occurred was found to be 71–75° F. on a dull day, and on a bright sunny day reached 88° F. in type (1) and 85° F. in type (2). There appears to be little difference in temperature and light between type (1) and type (2).

The pH of the water showed a slight gradation from a higher figure in type (1) to a progressively lower figure in type (2), but this factor varied considerably with the weather. In February the average of four readings in type (1) was 6.2 and of twenty-one in type (2) was 5.9, the lowest of this last series being 5.6 at the point farthest from type (1). In March 1932 the pH of the observation pools was lower, and those in type (1) showed a little surface scum, indicating stagnation of the water. In this case the pools in type (1) had a lower pH (5.3), and the next four pools, where the water was moving, varied between 5.5 and 6.0; the reading for the last pool was 5.4. In September 1932 a complete series of pH readings was taken throughout nearly the whole length of the drain (about 5 miles) at intervals of 1000 ft. The pH near pool 1 was 5.7, the highest pH (3000 ft. down the ditch) was 6.0. The first 7000 ft. had an average pH of 5.8, and the remainder varied from 4.8 to 5.1, with an average just below 5.0. The last 5000 ft. had a uniform pH of 5.0 and extended to the beginning of the *Limnophyton* region.

The total organic matter which was able to pass through a No. 42 Whatman's filter-paper was estimated on three occasions in pool 2 (type 1) and in pool 16 (end of type 2). The method devised by Dr Griffith, Assistant Agricultural Chemist, and described by him in the Appendix, is not a rapid one, so that he was only able to spare time for a small number of determinations. The average of three determinations at different seasons was 0.00236 gm. of carbon per 100 c.c. in pool 2 and 0.0066 in pool 16. The last determination in each case was 0.0038 and 0.0039 respectively; these were taken at a time when the water in pool 2 had been somewhat stagnant and a new drain entering the ditch below pool 2 had affected the colour of the water as far as pool 16. Throughout most of the year type (1) had a low organic content, whereas the remainder of the ditch (type 2) had a higher organic content.

(c) *Slashed Phoenix swamp (type 3).*

This area was originally *Phoenix* swamp but was cut over with the intention of planting with *Eucalyptus*. The palms, however, grew so rapidly together with the papyrus that it was decided that planting would be too costly. The pools in this area were frequently dry for considerable periods.

This habitat contained a considerable number of species, but rarely in large numbers. In this type were found *Culex semibrunneus*, *C. rubinotus*, *C. kingianus* and the only identified specimen of *C. andreanus*. *Anopheles implexus* occurred only in this area and in the true *Phoenix* swamp; *Anopheles coustani* was present, but only in small numbers. The common species of *Culex* at Namanve (*C. annulioris*, *C. guiarti* and *C. univittatus*) were rare or absent. The apparently large number of *Aedes* (*Banksinella*) *lineatopennis* is due to a collection of sixty larvae in one pool on one occasion. The losses of larvae (referred to on page 205) were probably greater for this habitat than for others, owing to the fact that the larvae of all the species of *Culex* mentioned were then unknown. Certain other species of *Aedes* (e.g. *Banksinella*, *Aedimorphus* and *Mucidus*) occurred in some numbers in this habitat and in the next.

These pools were heavily shaded, the time given by the Watkins' meter being from about 6 to 10 min., a great contrast to type (1). The temperature of the water was consequently lower (66–67° F.). The pH was variable, lower when the pools were nearly dry, and higher after rain, 4·6–5·3 in the first instance and 5·7–5·9 in the second. Organic matter was not estimated.

(d) *Phoenix swamp (type 4).*

The fauna of this type of swamp showed a general resemblance to that of type (3). *Anopheles implexus* was again present, and *A. coustani* occurred but in still smaller numbers. The temperature of the water was practically the same as in type (3) but the light was somewhat less intense, the paper in the Watkins' meter requiring 15 min. to darken. These pools, also, were frequently dry, and when full usually contained at least some surface water. The pH was only recorded on one occasion and was 5·5.

(e) *Cut Miscanthidium swamp (type 5).*

The pools in this type contained water during practically the whole year. The commonest mosquito was *Culex univittatus*; *Anopheles coustani*, *Culex annulioris* and *C. guiarti* were not uncommon. Two records of *Anopheles gambiae* are doubtful; in one case the collector's report stated that no Anophelines were present, and in the other instance personal search failed to confirm the presence of this species in the pool from which it had been recorded and in the neighbouring pool.

In Table I this type of habitat is divided into two columns, A and B, because the relative numbers of the species found in the three pools tabulated

under B are much more similar to those found in type (6), the pools of which were situated comparatively close to those of type (5 B).

All the pools in the habitat were brightly illuminated though not so exposed as the main ditch. The meter required 5–8 sec. to darken and, under the grass on the shady sides of some of the pools, up to 50 sec. The temperature rose to 84° F. on a bright day. The organic matter was estimated three times in two of the pools and with one exception varied from 0.0051 to 0.0059; the exceptional reading (0.0021) was given with some reserve by Dr Griffith and is perhaps best discarded.

(f) *Pools in recently burned papyrus (type 6).*

The fauna of these pools consisted of *Anopheles coustani*, *Culex annulioris* and *C. guiarti*; *C. univittatus* occurred in small numbers.

These pools had sides of black mud when observations were commenced. Very soon grasses began to grow among the slashed papyrus and the pools became more like those of types (5) and (7), but the last were frequently dry whereas the type under consideration usually contained water.

The two earlier estimations of organic matter in one of these pools gave 0.0087 and 0.0080, a later estimation when the grasses had grown round them gave 0.0050.

The pH of the pools varied from 5.2 to 6.2; after dry weather the reading was 5.2–5.4, and on two other occasions 5.6–6.2. The pools were at first fully exposed to the sun (meter-reading 2½ sec.), but later received some shade at the edges from grasses and papyrus.

(g) *Pools in papyrus swamp, burned earlier (type 7).*

These pools were of a more temporary nature than those in type (6), and this is reflected in the dominance of *Aedes lineatopennis*, which occurred abundantly in April, June and October 1932. *Culex univittatus* was also common; *Anopheles coustani* was very rare. Towards the end of the period these observation points had practically ceased to be pools, becoming almost uniform with the general level of the now nearly dry swamp.

The pH of such pools was variable; fourteen sites in this type of swamp were examined in March 1932 and gave pH readings varying from 5.5 to 6.2. The pools were fully exposed to light in most cases, but shady portions could be found where readings of from 10 to 20 sec. were recorded. The temperature in shady pools on a bright day was about 75° F., and in those in full sunlight about 85° F. No estimate was made of organic matter.

(h) *Pools in virgin papyrus (type 8).*

Three of these pools were artificially deepened in order to obtain more records than would be possible if the pools dried up. The pools of this type are characterised by the presence of various species of *Uranotaenia* and of *Hodgesia sanguinea*, but are by no means devoid of *Anopheles coustani*.



Photo. W. J. Eggeking

Phot. 3. Recently burned papyrus (habitat type 6) just before planting and when observations were begun.

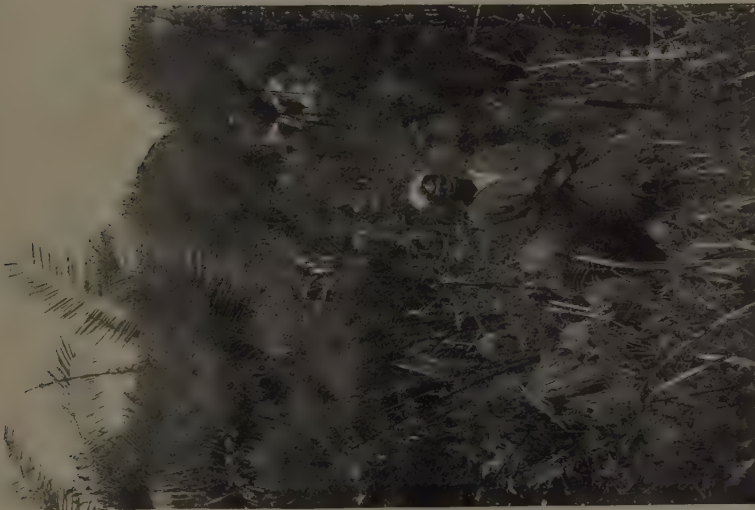


Photo. W. J. Eggeking

Phot. 2. The slashed *Phoenix* swamp showing tall papyrus and *Phoenix* which had grown after slashing. Post marks path to observation pool.

A number of specimens of the first two genera were lost in attempts to breed out and separate the various species. The pH of these pools was low (4.6–5.0), but after the papyrus was burned off for planting it rose a little (4.8–5.3). The temperatures were moderate, 69–72° F. when the pools in cut papyrus (type 6) were reading 84–85° F., and 64–65° F. on a dull day when these latter were reading 79–80° F. The organic matter of one of these pools was estimated on two occasions as 0.0059 and 0.0096; after the swamp had been burned the organic matter in the same pool was estimated as 0.0049.

(i) *Virgin Miscanthidium* (type 9).

The fauna of these pools shows a considerable resemblance to that of virgin papyrus in that *Uranotaenia* spp., *Corethrella* and *Hodgesia sanguinea* were present in both. This last species also occurred in pools in cut *Miscanthidium*, including a small pool of pH 4.3 near which a species of *Drosera* was found growing. There is also some resemblance to the fauna of the *Phoenix* swamp and slashed *Phoenix* swamp associations, both of which were also shady and both of which shared with the virgin *Miscanthidium* the presence of *Culex kingianus* and *Aedes tarsalis*. *Culex annulioris*, *C. guiarti* and *C. univittatus* are absent or rare in all these associations. Virgin *Miscanthidium* differs from the two *Phoenix* associations in the absence of *Anopheles implexus*, but the numbers of this species collected are not sufficiently great to be significant.

(j) *Vegetational zones at the lakeward end of the swamp.*

This section includes Eggeling's zones (i), (ii), (iii) and (iv) (lily zone, fringing papyrus, fern and sedge and the *Limnophyton* swamp). The area was not kept under regular observation but a few collections were made in it. They were made in the lily zone at Namanve on only one occasion and no mosquito larvae were found, but at Jinja, about 50 miles further east, collections were made in this zone by Mr T. W. Chorley: *Anopheles pharoensis* occurred abundantly among floating islets of dislodged lily roots, though not among the growing lilies; *A. coustani* also occurred, but in smaller numbers.

In the fringing papyrus on the lakeward side (at Namanve) were found larvae of *Anopheles moucheti* and *A. coustani*; on the inside of this fringe *A. coustani*, *Culex poecilipes* and *C. guiarti* occurred. It is possible that *Anopheles funestus* occurs here with *A. moucheti*, as it has been found on the lakeward edge of papyrus and other vegetation at Entebbe (Hancock, 1930) and at Jinja; the larvae are notoriously difficult to find.

In the fern which forms part of the floating mats of vegetation were found *Anopheles coustani*, *Uranotaenia balfouri*, *U. ? pallidocephalus*, *Culex univittatus*, *Hodgesia sanguinea* and *Ficalbia (Ingramia) uniformis*. In this type of swamp larvae were found chiefly among the fern and not at all in the more open pools. On one occasion a few larvae of *Culex annulioris* were found in filamentous green algae among the sedges and grasses.

Collections in the *Limnophyton* area have given negative results except on one occasion, when larvae of *Anopheles coustani* occurred; this latter area is rich in decaying vegetable refuse and black mud and does not dry out. It has not been possible for samples of the water to be analysed nor has the pH been recorded.

(k) *Forest pools.*

The fauna of these was collected by the writer, by Mr W. W. Soundy (Science Tutor, Makerere College) and on several occasions by Mr G. H. E. Hopkins (Entomologist) before work was commenced at Namanve; collections of adult mosquitoes found in the forest were also made. The work could only be done in spare time and it was necessary to go considerable distances to examine the swampy types of forest. The ground was usually soft mud with a high proportion of clay and often bordering on a stream. The mosquito fauna was largely influenced by the fact that rains caused the streams to rise and flood the forest; the floods gradually subsided leaving pools in which most of the larvae collected were found. The vegetation around the pools was usually dominated by *Clinogyne* with some *Phoenix reclinata* and a few saplings; occasionally a pool would be found at the roots of a tall tree, which contributed to the very dense canopy found throughout this type of forest. Fallen leaves were also examined.

The species found as larvae in these forests were: *Anopheles implexus* Theo., *A. obscurus* Grunb., *Aedes* (*Aedimorphus*) *domesticus* Theo., *A. (Banksinella) palpalis* Newst., *A. (Aedimorphus) punctothoracis* Theo., *Culex inconspicuus* Theo., *C. ? rubinotus* Theo., *C. (Lutzia) tigripes* Grp., *Eretmopodites grahami* Theo., *E. oedipodius* Grah., *Ficalbia (Ingramia) nigra* Theo., *F. (Mimomyia) plumosa* Theo., *Uranotaenia* spp. (at that time indeterminable).

The following species were obtained as adults: *Aedes (Stegomyia) apicoargenteus* Theo., *A. domesticus* Theo., *A. tarsalis* Theo., *Eretmopodites* spp. (females, probably of the above two species), *Mansonia annetti* Theo., *M. aurites* Theo., *M. maculipennis* Theo., *M. fuscopennatus* Theo., *M. metallicus* Theo.

Of the larvae collected, *Anopheles implexus* occurred invariably in pools, *A. obscurus* chiefly in a stream among debris and floating leaves of *Clinogyne*, but also in a series of pools which appeared to have recently formed a stream. *Culex inconspicuus* was a common species in pools but was never recorded from Namanve. *Aedes palpalis* occurred very abundantly on one occasion in a pool at the edge of a tract of forest. The two species of *Eretmopodites* occurred commonly in water retained in large fallen leaves.

Larvae of *Aedes apicoargenteus* and of *Culex nebulosus* were found in tree holes in the forest fringing Namanve swamp.

(l) *Collections of adult mosquitoes at Namanve.*

Collections were made in native huts to ascertain whether the apparent absence of *Anopheles funestus* from the swamp was real; the only species of *Anopheles* found in the huts was *A. gambiae*. These huts were too far from the lake edge for *A. moucheti*, or other Anophelines occurring in that zone, to be found in them.

IV. GENERAL CONCLUSIONS ON THE IMPORTANCE OF PHYSICAL FACTORS.

The factors measured have been hydrogen-ion concentration (pH), carbon, iron, temperature and light. These are influenced by the vegetation so that they are indirectly in part biological.

(a) *Hydrogen-ion concentration.*

The pH of the various pools was not constant, but on comparing the observations of any series there is a tendency for the greater acidity to be associated with stagnation or peatiness. *Anopheles gambiae* may perhaps be said to avoid the more acid waters, but only when this factor is associated with high carbon in true or colloidal solution. Pomeroy (1931) has recorded finding this species in natural waters with a pH as low as 4.0. *Hodgesia sanguinea* appears to be found in the more acid pools but there is not a similar correlation with peatiness. A series of observations on pH (carried out in March 1932) which included the observation pools, and a series on these pools alone (undertaken in August of the same year) gave the following results:

Type of habitat	No. of observations	Average pH	Highest pH	Lowest pH
Main drain in slashed <i>Phoenix</i> swamp (type 1)	March: 4 August: 2	6.2 6.7+	6.3 6.7+	6.1 6.7+
Pools in freshly burned papyrus (type 6)	March: 7 August: 3	6.0 6.0	6.1 6.2	5.6 5.7
Main drain in papyrus and <i>Miscanthidium</i> (type 2)	March: 21 August: 5	5.9 5.7	6.1 5.9	5.6 5.5
Pools in slashed <i>Phoenix</i> swamp (type 3)	March: 4 August: all pools dry	5.8	5.9	5.7
Pools in papyrus swamp burned earlier (type 7)	March: 14 August: all pools dry	5.7	6.2	5.5
Pools in cut <i>Miscanthidium</i> swamp (type 5)	March: 27 August: 10	5.5 5.1	5.9 5.0	5.1 4.8
Pools in virgin <i>Miscanthidium</i> (type 9) and papyrus (type 8)	March: 16 August: 8	4.7 4.9	4.9 5.0	4.6 4.6

(Type (9) averaged 5.1 and type (8) 4.8 in August.)

By March 1933 considerable changes had taken place; types (8) and (9) had been cut and burned and the pH ratio of the other pools had changed. This change was not operating for a sufficient period to affect the figures in Table I. Except in types (2) and (5), very few larvae were found at this time and many of the pools were dry. The averages for the readings taken were: type (1) 5.3, type (6) 5.3, type (2) 5.6, type (3) dry, type (7) (2 readings only)

5.1 and 5.2, type (5) 5.2. An examination of a sphagnum bog at Nabugabo, about 50 miles west of Namanve (see Eggeling, 1935) revealed larvae of *Anopheles coustani* at a pH of about 5.0 (British Museum Monograph).

The alkali reserve was estimated in one of the pools in the virgin papyrus (type 8) at Namanve and was found to be 0.00075 (Lake Victoria being 0.00171 in the Kavirondo Gulf; Graham, 1929); at Nabugabo the alkali reserve was not more than the figure, 0.000286, given by Worthington for the contiguous lake.

(b) *Organic matter (carbon) in solution.*

The carbon estimations are mentioned under the different habitats and are arranged below in ascending average values. The water was filtered through a No. 42 Whatman filter paper and it is probable, therefore, that carbon derived from living bacteria is included.

	gm. carbon per 100 c.c.
Main drain in slashed <i>Phoenix</i> swamp (type 1)	0.00236
Pools in cut <i>Miscanthidium</i> swamp (type 5)	0.0050
Main drain at some distance from beginning of swamp (type 2)	0.0066
Virgin papyrus (type 8)	0.0068
Recently cut and burned papyrus (type 6)	0.0071

The difference in the amounts of carbon found in the last three types of pool mentioned above is small. The average for the pools in the recently cut papyrus was in all probability unduly raised by the digging up of the black mud when the trees were planted. It is probable that, over an extended period, the pools in the virgin papyrus association would be found to have a constantly higher organic content than the other types of pools examined.

The indications obtained from the above figures are that, during the period of the observations, organic matter in the main drain in the slashed *Phoenix* swamp was low, and that it was higher throughout the rest of the swamp, the average figure obtained in the cut *Miscanthidium* being lower than that in the papyrus.

Anopheles gambiae clearly appears to prefer water containing a low organic concentration. This is confirmed by the observations of the writer on the effect of the addition of township refuse (Hancock, 1930), by the experiments recorded by Hopkins (1933) in which organic matter was increased by introducing cut elephant grass into pools breeding *A. gambiae*, and by observations at Luzira swamp (Hopkins, 1934) where *A. gambiae* was found to be absent from peaty water. Hopkins (1933) notes the change from an Anopheline to a Culicine fauna (mainly *Culex pipiens*), when elephant grass was added to the pits in which *Anopheles gambiae* was breeding. This is strikingly borne out by the observations made at Namanve if a comparison is made between the faunas of the two sections of the main drain (types 1 and 2). From Table I it is clear that *Culex annulioris* and *C. guiarti* appear in large numbers where *Anopheles gambiae* is practically absent; the reason for the presence of this

last species at all in type (2) is discussed above. It must, however, be added that *Culex annulioris* is often associated with filamentous algae, and Mr Hopkins informs the writer that this association is almost invariable. The absence of this species from pools in type (1) may have been due to their containing less algae, but though plants of this kind were frequently found in type (2) observations were not made as to their presence in type (1).

There is an apparent discrepancy between the negative correlation of *Anopheles* larvae with organic matter found at Namanve and the positive correlation found by Harvey and Symes (1931). Unfortunately the two methods of estimation are not comparable and it was impossible for Dr Griffith to find time to estimate the water by both methods. The method used by Harvey and Symes is designed merely to give comparative figures, and not absolute results such as are obtained by the method employed at Namanve.

It is probable, however, that the theory of inadequate suitable food, put forward in this paper, applies equally in Kenya, the pools with very low organic content being not merely lacking in suitable food but nearly sterile. Unfortunately Harvey and Symes do not state whether the pools which contained no species of *Anopheles* were also devoid of Culicine mosquitoes and other animals which feed on micro-organisms. There is doubtless an optimum organic content of water for the breeding of Anophelines, and it may well be that the breeding places without Anophelines described by Harvey and Symes deviated from this optimum by having too little organic matter, while it is almost certain that those at Namanve deviated by having too much.

The influx of surface water into Namanve was correlated with the presence of large numbers of *A. gambiae*, just as occurred in Kenya, but as the water with which the surface water mixed was peaty, the total organic content was reduced; in the Kenya results the proportion of organic matter in the standing water seems to have been low, since the authors state that "after a dry period it appears that heavy washing rains result in the addition of considerable quantities of organic matter and the organic index rises immediately. It falls as rapidly immediately afterwards."

(c) *Iron in solution.*

The writer suggested in a previous paper (Hancock, 1930) that the absence of Anopheline mosquitoes might be correlated with a high concentration of dissolved iron salts. The concentration of iron in solution at Namanve was very low, rarely exceeding 2-3 parts per million, although iron could occasionally be found in scums where the water was stagnant (but not in solution in the water below the scum). It may be that in some swamps iron is present only where there is a high organic content in the water, and this is a point requiring further study.

The position with regard to iron or peatiness cannot be regarded as scientifically satisfactory, though even our present knowledge is of considerable

practical value. It may be that none of the factors discussed is the true explanation of the requirements of different species of mosquito larvae, and a factor not studied at Namanve, such as nitrogen in some form of combination (as suggested by Beattie and Howland, 1929) may give a true correlation.

(d) *Food factors.*

The whole question as to the true limiting factor or factors requires careful experimental study and little of this work has been possible so far. In the laboratory in Kampala the writer has endeavoured to breed larvae of *Anopheles gambiae* in water from pool 16 (the last pool in the main ditch, type 2) without success. The addition of a little powdered yeast to this water is, however, quite sufficient to enable the larvae to complete their life cycle. There does not, therefore, appear to be anything toxic in water of this type but merely an unsuitable food factor. It must, however, be admitted that in the laboratory the pH of this water rises and there is not the constant renewal of the products of decay, coming from the mud below, which occurs in nature. This change in pH might result in the death of the natural microflora occurring more rapidly than the growth of suitable food organisms proper to a somewhat higher pH (MacGregor, 1929). The experiment therefore requires repeating at a constant pH, perhaps best maintained by a slow stream of CO₂, which is a likely factor to be lost when the water is put into a jar and removed from the decaying mud of its place of origin. Even the addition of mud to the jars may not give natural conditions, and it was not found to be sufficient to bring about the survival of larvae. The writer suggests that there is a true lack of suitable food for *A. gambiae* in these swamp waters, and that the occurrence of this species in the main ditch at Namanve was governed by the presence of food carried along with surface water entering from the top of the swamp.

In the fringing papyrus near the other end of the ditch, where the fresh lake water meets the swamp water, *A. moucheti* appears; this, again, suggests an extraneous food supply, in this case from the lake edge. It is difficult to conceive conditions with more decay than in the warm permanent pools, containing much black mud, in the *Limnophyton* zone; these pools have not yet yielded any mosquitoes. It is possible that the oxygen factor would repay careful study in such pools.

(e) *Light and temperature.*

It is not possible to separate these two factors completely. In shady pools the temperature is more constant than in those exposed to full sunlight, and never rises so high as in these latter. The surface of the pools (the part where the mosquito larvae are usually found) becomes warmer than the lower layers, so that in all cases temperatures were taken with the bulb of the thermometer just submerged.

Apart from overhead shade, lateral shade becomes important for a few hours of the day when the sun is low. Cloud had an important effect in exposed

pools but influenced the temperature of shady pools to a much less degree. When ditches were being cleaned out or if a pool was disturbed the consequent mixing of the lower layers of water with the upper layers caused a reduction in the surface temperature.

Since the observation points were scattered over a wide area, so that it took a considerable time to visit them all, the two series of temperature readings (although all taken, in each case, on one day) cannot be strictly comparable; the error from this cause is probably in the nature of 2-3° F. Taking this into account, the differences between certain types of habitat remain significant.

Light was only estimated once in each pool. When most of the pools had been done a storm came up and the remainder of the readings had to be deferred to another occasion when, unfortunately, the sunlight was rather more diffuse.

The observations made are shown in Table II.

Table II. *Showing observations on temperature and light in different types of habitat: A, on a bright day; B, on a duller day. The times given are those required for the Watkins' meter to darken.*

	Temperature ° F.	Light	
		Exposed centre	Shady edge
Main ditch (type 1)	A 77-88 B 73	2½ sec.	20 sec.
Main ditch (type 2)	A 78-85 B 71-75	2½ sec.	20 sec.
Recently slashed papyrus (type 6)	A 84-85 B 79-80	2½ sec. (a)	—
Slashed <i>Miscanthidium</i> (type 5 A)	A 76-84 B 67-73	2½-8 sec.	50 sec.
Slashed <i>Miscanthidium</i> (type 5 B)	A — B 76-79	—	—
Slashed papyrus (type 7)	A 75-85 B Dry	5-11 sec.	20 sec.
		Whole of each pool shaded	
Virgin papyrus (type 8)	A 69-72 B 64-65	1 min. 20 sec. to 2 min. 20 sec. (b)	
Virgin <i>Miscanthidium</i> (type 9)	A 68-70 B 61	5-10 min.	
Slashed <i>Phoenix</i> swamp (type 3)	A 66-67 B Dry	6-10 min.	
<i>Phoenix</i> swamp (type 4)	A 67-68 B Dry	15 min.	

(a) and (b). These pools were estimated at a later date; (a) is calculated from the results of the earlier series, but (b) is the observed figure and is probably too high; at the time when this group of observations was made the sun had scarcely penetrated the thin clouds. A reading of about 1 min. is perhaps a fair estimate for the pools in virgin papyrus.

In all pools mosquito larvae were able to avoid direct sunlight, but the ditches, especially where recently cleared, did not give quite so much shade as the pools. Some of the latter were slashed over at intervals, thus periodically lessening the amount of shade of which the larvae could take advantage. The

virgin papyrus was intermediate in character, while the *Miscanthidium* and *Phoenix* zones were dark. The temperatures fell into two groups, the virgin papyrus (intermediate in light) being included in the cooler group.

Repeated observations in Uganda have shown that *Anopheles implexus* is a shade-loving species. Other species preferring the shady pools at Namanve have been *Uranotaenia balfouri*, *Aedes tarsalis* and *Culex kingianus*, while those which appear to dislike these conditions are *C. annulioris*, *C. guarti*, *C. pallidocephalus* and to a lesser extent *C. univittatus*. *Anopheles gambiae* is known from other observations to prefer unshaded waters. The figures show a probability that *Aedes domesticus* prefers shady conditions, and this is confirmed by the frequency with which adults are encountered in forests.

Anopheles obscurus has been found in Uganda only in cool water in forests and has only been bred with difficulty in the laboratory by the use of a "butter-cooler." The absence of *Culex inconspicuus* from *Phoenix* swamp at Namanve cannot be explained.

V. BIOLOGICAL FACTORS.

The above physical factors cannot be completely dissociated from the plant communities, which are more probably the cause of these factors than the result of them. The more intimate associations with the mosquitoes of insects or fish which prey on their larvae or compete with them for food, cannot properly be ignored and may prove to be factors modifying the conclusions given above. It is hoped to give some account of the Dytiscidae in a later paper, but our knowledge of the other aquatic forms is very fragmentary and the complete absence of any means of identifying the larvae of most of the forms makes a comprehensive ecological study out of the question.

A further factor is that of the food of the adult mosquitoes: the absence of a species might well be due to the adult finding no suitable vertebrate host on which to feed in the neighbourhood of Namanve swamp.

VI. SEASONAL PREVALENCE.

The total output of the commoner mosquitoes from Namanve swamp is given in Table III. This table gives little information which can be correlated with any of the factors mentioned above, because it is impossible to separate those due to the absence of water and consequent cessation of breeding from those due to changes going on in the pools which still contained water. It was also impossible to make sufficient observations on chemical, physical and biological factors to give any seasonal correlations. The table is, however, of value in indicating to an epidemiologist at what seasons potential vectors of disease originating in such a swamp are likely to be more abundant.

On examining the detailed records of the pools it is possible to suggest certain correlations with rainfall, both in those pools which were permanently full of water and in those which frequently dried up. *Anopheles gambiae*



Photo. W. J. Eggeling

Phot. 4. An observation pool (no. 10) in same habitat as phot. 3 after young trees had been planted and vegetation had grown again to a considerable height. Main ditch in foreground.

occurred only in the main ditch; this was never dry but there is an indication that *A. gambiae* was more abundant after rain, which supports the correlation with physical or food factors suggested above. After the dry months December 1932 to February 1933, the numbers of *A. gambiae* were such as to indicate that the higher organic content (0.0038 carbon) was excessive for the development of the larvae. This species is well known to breed abundantly in types of temporary pools other than those investigated at Namanve.

Table III. *Seasonal output of the commoner species of mosquitoes from March 15th, 1932 to March 29th, 1933, tabulated by calendar months; totals of forty-four pools except for March 1932 when only thirty-two pools were collected. Those omitted, however, contained few of the commoner species of mosquito larvae.*

	<i>Anopheles coustani</i>	<i>Anopheles gambiae</i>	<i>Aedes lineatopennis</i>	<i>Aedes tarsalis</i>	<i>Culex annulirostris (or C. aurantapez)</i>	<i>Culex guianae</i>	<i>Culex kingianus</i>	<i>Culex rulinolus</i>	<i>Culex univittatus</i>	<i>Uranotaenia balfouri</i>	Rainfall (in.)
1932:											
March	121	5	0	0	2	6	0	2	303	0	10.25*
April	123	14	38	0	210	22	3	1	152	10	4.79*
May	276	37	31	0	107	78	15	14	238	8	4.81*
June	501	23	136	24	64	65	4	6	128	12	1.92
July	200	12	0	0	4	33	18	28	27	0	2.98
August	285	0	0	1	11	43	15	16	125	4	2.23
September	263	7	56	11	22	65	1	66	133	0	5.16
October	130	1	169	28	105	20	14	52	225	36	6.52
November	167	39	82	8	69	7	3	13	239	52	6.67
December	219	14	3	6	136	16	2	3	138	16	2.45
1933:											
January	75	0	0	0	54	35	0	1	72	0	2.44
February	40	0	0	8	2	7	0	0	74	0	3.69
March	59	5	0	0	30	13	0	0	82	0	7.50

* Records from Kololo Meteorological Station 7 miles from Namanve swamp; at this station the rainfall for January and February 1932 was 0.61 and 0.72 in. respectively.

Certain species of *Aedes* (subgenera *Aedimorphus*, *Banksinella* and *Mucidus*) occur almost exclusively in temporary pools, where they appear in large numbers after rain. On referring to Table I these are found to be confined to pools of a type which frequently dried up, notably type (7) but also types (3), (4) and (9). Other mosquitoes also occurred in the temporary pools, and for this reason showed marked differences in numbers at different seasons, but were found in permanent pools as well.

VII. SUMMARY AND CONCLUSIONS.

Namanve swamp contains a considerable mosquito fauna which varies according to the nature of the different parts of the swamp and with the work of reclamation.

The factors of pH, light, temperature and organic matter are considered, and some of these have been correlated with the presence or absence of certain species of mosquitoes.

From the viewpoint of the malariologist Namanve swamp was originally entirely innocuous except for a very narrow fringe of papyrus (the fringing papyrus zone) where *Anopheles moucheti* and probably also *A. funestus* occur. It was only when reclamation began that conditions became suitable for *A. gambiae* and this only to a very limited extent¹.

It has been shown by Eggeling (1934, 1935) that at Namanve there is a direct transition from *Miscanthidium* or papyrus swamp to *Phoenix* swamp. In other swamps there is an intervening grass zone and from the point of view of the malariologist this is probably the zone of greatest importance. The writer's observations at Entebbe indicated this, but at Entebbe springs were flowing into such a grass zone. The critical factor appears to be that of organic matter; if rain or springs induce in a grass zone, where the light is already intense, a considerable dilution of the organic matter in solution or carry with them suitable food organisms, then this grass zone is the critical area.

VIII. ACKNOWLEDGMENTS.

The writer wishes to express his thanks to Mr G. H. E. Hopkins for considerable assistance in the preparation of this paper and for permission to refer to certain observations which he is including in a forthcoming monograph on Ethiopian mosquitoes to be published by the British Museum. Mr Hopkins has also identified all the more difficult mosquito larvae and many of the adults. All doubtful adult mosquitoes have been submitted to Dr F. W. Edwards for examination and his help is gratefully acknowledged. Mr T. W. Chorley has greatly assisted by identifying many of the better known larvae and by supervising the mounting and preparation of material for examination. Mr W. J. Eggeling assisted the writer in choosing the observation pools and in making a number of determinations of pH. The routine collections were made by Erika Kasozi except when his other duties necessitated another boy being detailed for the work.

APPENDIX.

ESTIMATION OF ORGANIC CARBON IN WATERS

By G. GRIFFITH, PH.D., B.Sc. (*Assistant Agricultural Chemist*).

The method used is that of Robinson, McLean and Williams² (1929), modified for liquids, and consists of oxidising the substance to be examined in a Kjeldahl flask fitted with a ground-glass stopper with two tubes, one of which

¹ Under different conditions afforestation may result in a temporary output of enormous numbers of *A. gambiae* (Hopkins, 1930). Mr Hopkins informs me that the water in the swampy area to which he refers was comparatively lacking in organic matter.

² Robinson, G. W., McLean, W. and Rice Williams (1929). "The determination of organic carbon in soils." J. Agric. Sci. 19, 315-24.

is attached to a filter flask in the neck of which is inserted an absorption tower with three platinum gauge baffles, the other tube being kept closed throughout the digestion. The oxidising agent is strong H_2SO_4 together with K_2SO_4 and a crystal of CuSO_4 as in the ordinary Kjeldahl digestion. SO_2 is evolved in the reaction and this is absorbed quantitatively by a $N/2$ solution of iodine in the filter flask. Digestion is continued for a quarter of an hour after the residue in the Kjeldahl flask has developed a pale green colour. Air is then swept through the apparatus by lowering a glass tube through the second tube in the stopper of the Kjeldahl flask below the surface of the liquid. The absorption tube is connected with an aspirator and air is slowly drawn through for an hour. The iodine remaining is then titrated against $N/2$ thiosulphate.

There is often a slight tendency to leakage at the ground-glass stopper. This may be rectified by attaching the aspirator and keeping a slight negative pressure inside the apparatus throughout the experiment. When digestion is complete the aspiration proper is then carried out as described above.

The modification for the present purpose renders it unnecessary to evaporate a bulk of liquid to dryness before making a carbon determination.

250 c.c. of the filtered unconcentrated liquid is placed in the Kjeldahl flask with the reagents. A second filter flask is interposed between the digestion and the absorption flasks. This serves to condense the steam that is driven off in the first heating. When the liquid in the Kjeldahl flask has attained a certain concentration, oxidation commences and SO_2 is evolved, and this is absorbed as usual by $N/2$ iodine solution. It is necessary to put some iodine solution into the condensing flask as well. For the final titration the contents of the two flasks are combined. (Results may be expressed in gm. carbon per 100 c.c. of the original solution.)

Blank determinations are carried out on an equal volume of distilled water with the same quantities of reagents.

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THE INFLUENCE OF BIOLOGICALLY CONDITIONED MEDIA ON THE GROWTH OF A MIXED POPULATION OF *PARAMECIUM CAUDATUM* AND *P. AURELIA*

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(With six Figures in the Text.)

I. INTRODUCTION.

THE displacing of one species by another is apparently connected with the advantages belonging to one of the competitors. In other terms one of them is relatively better adapted to the habitat. The problem of relative adaptation has been recently analysed theoretically by Fisher (4), but in spite of its general interest it has hitherto been very insufficiently investigated on concrete biological examples.

The present paper is an account of the investigation on relative adaptation in two species of Infusoria—*Paramecium caudatum* and *P. aurelia*—under different conditions and at different stages of population growth. The case of two similar species simplifies the analysis of certain general regularities of competition in comparison with the study of similar races belonging to the same species.

Certain interesting observations showing the dependence of the relative adaptation of two species of animals on environmental conditions have recently appeared in ecological literature. For instance, Beauchamp and Ullyott (3) have shown that when two species of *Planaria* in the English Lake District occur in competition with one another, temperature is the factor which governs the relative success and efficiency of the two species. Timoféeff-Ressovsky (9), dealing with the two species of fruit-fly *Drosophila*, has arrived at the same conclusions. We have studied in this paper the action of biologically conditioned media, containing waste products of the organisms that have lived in them before.

We had to deal with the influence of homotypic and heterotypic conditioning (produced by organisms of the same and of a different species) on the growth of a mixed population. As Woodruff (10) showed in his classical paper, heterotypic conditioning in certain cases has much less influence on the rate of reproduction of Infusoria than homotypic conditioning. In the papers which have appeared since, the question of species specificity of the conditioning has not attracted the attention it deserves—as Allee (1) has

pointed out in his recent review. This author has summarised the literature dealing with this subject (1, 2), and there is no need to repeat it here.

II. METHODS.

Our investigations were carried out in the laboratory. The conditions of the experiments were, however, somewhat complicated, closely approaching those of nature. The nutritive medium was prepared in the following manner: to 500 c.c. of the Osterhout salt solution¹ 2.5 gm. of hay were added, boiled for 30 min., filtered and sterilised. A pure culture of the bacterium *Bacillus proteus* was inoculated and the medium was divided into two parts: one of them being populated by a pure culture of *Paramecium caudatum*, and the other by *P. aurelia*. After the cessation of population growth in both cultures and on their approaching "saturating levels" (about the 11th day at 26° C.), the liquid was carefully freed from *Paramecia* by filtration, and served as a "biologically conditioned medium" for our experiments. One of these media contained the waste products of *P. caudatum*, and the other those of *P. aurelia*. Into 100 c.c. of such a "biologically conditioned medium" a determined quantity of yeast cells, *Saccharomyces exiguus*, taken up by a platinum loop from the solid medium, was introduced for the nutrition of the *Paramecia*.

10 c.c. of the liquid were poured into each test-tube and stopped by a cotton-wool plug. On the medium of *Paramecium caudatum* as well as on that of *P. aurelia* three groups of experiments were arranged: (1) the growth of *P. caudatum* in pure culture (initial population 25 individuals per 10 c.c.); (2) the growth of *P. aurelia* in pure culture (inoculation=25); and (3) the growth of a mixed population of *P. caudatum* and *P. aurelia* (inoculation=25+25). The experiments were made in a thermostat at 26° C.

There are two phases in the changes of the population under such conditions: (1) competition between the two species for the utilisation of a certain limited amount of the nutritive substances introduced at the beginning of the experiment. This stage has already been analysed by Gause on yeast cells (6) and on several Protozoa (7, 8). But after the cessation of growth, stage (2) begins: that is the dying out of the population. The investigation of the dynamics of this process has shed some light on certain features of the comparative adaptability of the species studied.

III. THE INFLUENCE OF BIOLOGICALLY CONDITIONED MEDIA ON COMPETITION FOR COMMON FOOD BETWEEN THE TWO SPECIES.

Table I represents the changes of density in the population per 0.5 c.c. (our counts were usually made on about 0.1 c.c. and then calculated for 0.5 c.c.). Each figure showing the number of individuals represents the mean

¹ NaCl 2.35 gm.; MgCl₂ 0.184 gm.; MgSO₄ 0.089 gm.; KCl 0.050 gm.; CaCl₂ 0.027 gm.; re-distilled water up to 100 c.c. This stock solution was diluted by re-distilled water 225 times its volume.

value for three cultures. In order to pass from the numbers of individuals to the biomasses (volumes) of our species it is sufficient to multiply the numbers of individuals of the smaller *P. aurelia* by 0.39 (see Gause, (8)).

Table I. *Changes in the density of population*
(numbers of individuals per 0.5 c.c.).

Days	Medium of <i>P. caudatum</i>			Medium of <i>P. aurelia</i>		
	<i>P. c.</i>	<i>P. a.</i>	<i>P. c./P. a.</i>	<i>P. c.</i>	<i>P. a.</i>	<i>P. c./P. a.</i>
1	3.5	5.5	2.5	4	3.5	7
2	28	42	18	14.6	24	14.6
3	70	56	36	30.5	66	29
4	114	228	64	61.5	88	59
5	132	144	56	73.4	108	61.3
6	130	182	50	76	150	61.3
7	136	222	82	86.7	110	61.5
8	151.5	220	77	87.4	175	60.7
9	—	—	—	—	—	—
10	152	192	78	82.6	154	37.4
11	86	230	68	72	162	38.7
12	146	198	62	64	126	52
13	98	182	28	57.5	116	13.3
14	50	116	18	17.3	166	21.3
15	38	120	10	10	144	4
16	8	54	2	4	108	1
17	—	42	0	—	96	0
18	—	26	0	—	30	0
19	—	28	0	—	40	0
20	—	44	0	—	16	0
21	—	30	0	—	18	0
22	—	30	0	—	14	0
27	—	52	—	—	10	0
28	—	56	—	—	14	0
29	—	28	—	—	4	0
30	—	26	—	—	2	0
31	—	20	—	—	—	0
32	—	10	—	—	—	0
33	—	6	—	—	—	0
34	—	—	—	—	—	0

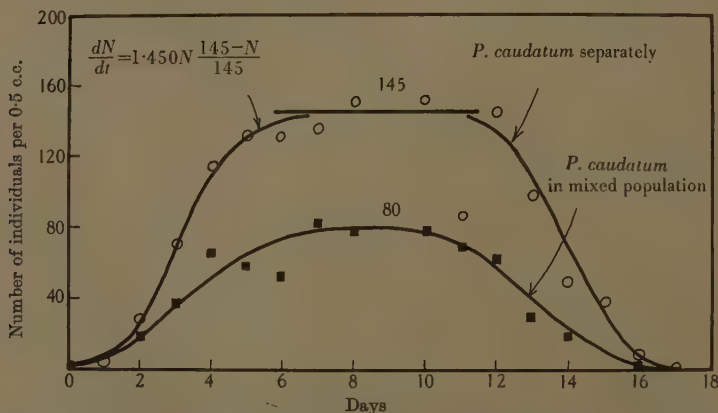


Fig. 1. The growth of *P. caudatum* in pure and mixed populations (medium of *P. caudatum*).

Figs. 1, 2, 3 and 4 show graphically the changes in the populations. One can see that the first stage—growth of the populations—is generally completed

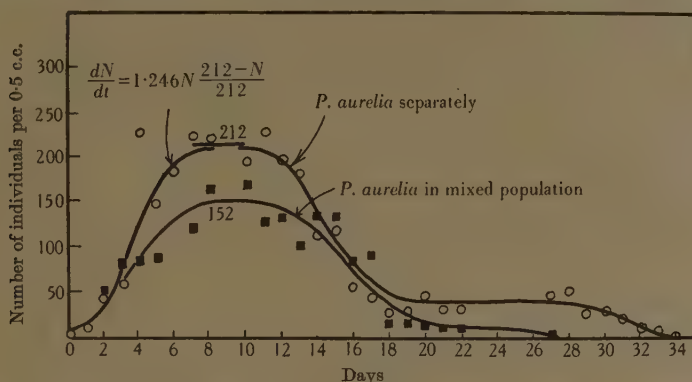


Fig. 2. The growth of *P. aurelia* in pure and mixed populations (medium of *P. caudatum*).

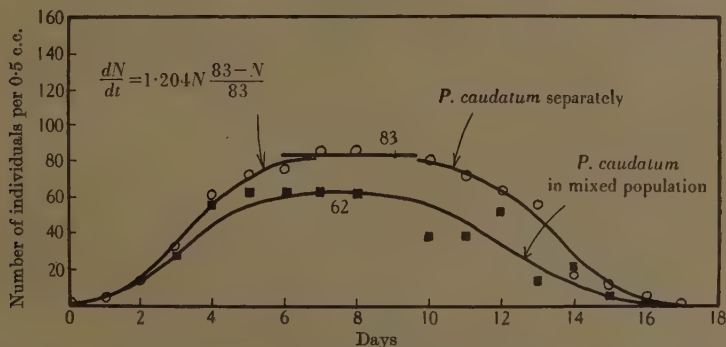


Fig. 3. The growth of *P. caudatum* in pure and mixed populations (medium of *P. aurelia*).

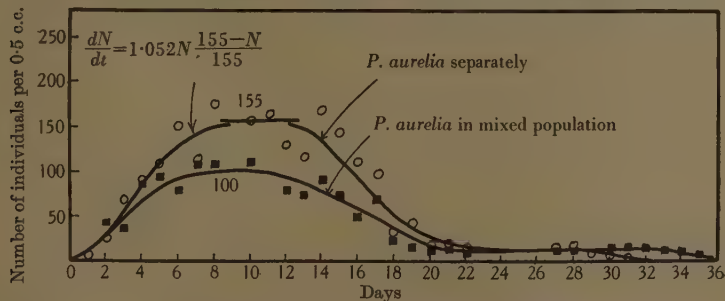


Fig. 4. The growth of *P. aurelia* in pure and mixed populations (medium of *P. aurelia*).

on the seventh day. The maximal level attained remains invariable up to about the tenth day, and decline of the population only begins later on.

Turning our attention to the first stage we may first of all consider the levels of the saturating populations under different conditions (Table II). It is evident that the medium of *P. aurelia* is less favourable for both species. The levels of population of *P. caudatum* (in pure and in mixed cultures) here are, correspondingly, 57.3 and 77.5 per cent., and of *P. aurelia* 73.1 and 65.8 per cent. From the relation between the levels of population of the same species in pure and in mixed culture it is possible to evaluate the degree of the depression of this species due to the other or, in other terms, its energy of competition under given conditions. As Table II shows, *P. caudatum* in a mixed culture on a "homotypic" medium attains 55.2 per cent. of the control, whereas on a "heterotypic" it attains 74.7 per cent. For *P. aurelia* correspondingly we find 64.5 and 71.6 per cent. Therefore our species on a homotypically conditioned medium "of their own" kind appear to be weaker in competition and are more strongly depressed in the struggle for existence.

Table II. *Levels of saturating populations under different conditions (K).
(Numbers of individuals per 0.5 c.c.)*

	In the pure culture (a)	In the mixed culture (b)	(b) as % of (a)
I. Medium of <i>P. caudatum</i>			
(1) <i>P. caudatum</i>	145	80	55.2
(2) <i>P. aurelia</i>	212	152	71.6
II. Medium of <i>P. aurelia</i>			
(1) <i>P. caudatum</i>	83	62	74.7
(2) <i>P. aurelia</i>	155	100	64.5

The latter question deserved further analysis. We therefore passed on from the numbers of individuals to their biomasses (as indicated above), and the calculated characteristics of population growth are given in Table III. Here we find the levels of saturating populations expressed in units of biomass (*K*) as well as the coefficients of multiplication (*b*). These coefficients characterise the rate of potential geometric increase of the population in the absence of any limitation as to the means of subsistence (conditions approximately fulfilled at the beginning of growth). They show an increase per unit of biomass per day; and a description of the method of calculation of these coefficients may be found in (5) and (6).

Table III. *Characteristics of the growth of populations expressed
in units of biomass (P. caudatum=1, P. aurelia=0.39).*

	<i>b</i>	<i>K</i>	Coefficients of the struggle for existence
I. Medium of <i>P. caudatum</i>			
(1) <i>P. caudatum</i> separately	1.450	145	$\alpha = 2.12$ (<i>P. a.</i> \rightarrow <i>P. c.</i>)
(2) <i>P. aurelia</i> separately	0.486	83	$\beta = 0.11$ (<i>P. c.</i> \rightarrow <i>P. a.</i>)
II. Medium of <i>P. aurelia</i>			
(1) <i>P. caudatum</i> separately	1.204	83	$\alpha = 0.63$ (<i>P. a.</i> \rightarrow <i>P. c.</i>)
(2) <i>P. aurelia</i> separately	0.411	60	$\beta = 0.20$ (<i>P. c.</i> \rightarrow <i>P. a.</i>)

Comparing the superiority of one species over another under different conditions, we note that in coefficients of geometric increase *P. caudatum* exceeds

P. aurelia on the medium "of its own" 2.98 times, and on the "strange" medium 2.93; in maximal biomasses correspondingly 1.75 and 1.38. The superiority of *P. caudatum* over *P. aurelia* is therefore more clearly apparent on homotypic (in this case generally less toxic) medium. In spite of this *P. caudatum* in competition with *P. aurelia* is relatively more depressed just on "its own" medium. We may thus see that in the complicated situation of these experiments the superiority of one species over another in competition does not simply reflect the properties of these species taken independently, but that it essentially depends on the processes of their interaction.

To clarify this point we can calculate the coefficients of the struggle for existence from the equation

$$\left. \begin{aligned} \frac{dN_1}{dt} &= b_1 N_1 \frac{K_1 - N_1 - \alpha N_2}{K_1} \\ \frac{dN_2}{dt} &= b_2 N_2 \frac{K_2 - N_2 - \beta N_1}{K_2} \end{aligned} \right\}.$$

It has been pointed out by Gause (6) that the coefficient of the struggle for existence α measures the degree of decrease of the unused opportunity for growth of the first species by a unit of biomass of another species (N_2) in relation to the action of its own unit of biomass (N_1). If, for instance, α is equal to 2, it means that every individual (in case of an equality of biomasses) of the second species occupies in the microcosm the place of two individuals of the first species.

The values of the coefficients of the struggle for existence (Table III) show clearly that the superiority of *P. caudatum* over *P. aurelia* in the coefficient of geometric increase on a "homotypic" medium is entirely absorbed by a strong inhibitory action of *P. aurelia* on *P. caudatum* ($\alpha=2.12$), and in this way results in a depression of the latter species.

We can note that under other conditions of cultivation (8) *P. aurelia* possesses a larger coefficient of geometric increase than *P. caudatum*¹. It has been shown by Gause (7, 8) that, if the food resources of the microcosm are maintained at a certain level and if the density of population fluctuates (rarefaction and subsequent growth up to a saturating level), the species possessing a greater coefficient of multiplication drives its competitor entirely out of the microcosm. Since under some conditions *P. aurelia* possesses a larger coefficient of increase, whereas under others *P. caudatum* has the advantage, it is evident that the ecological situation may completely reverse the direction of the change in the mixed population.

¹ This takes place in media containing pathogenic bacteria, *Bacillus pyocyaneus*, and is apparently connected with the resistance of *P. aurelia* to an accumulation of their waste products (see section IV).

IV. THE INFLUENCE OF BIOLOGICALLY CONDITIONED MEDIA
ON THE DECLINE OF POPULATIONS.

Figs. 1, 2, 3 and 4 represent also the dying out of population. For the analysis of this process we have taken the level of the saturating population

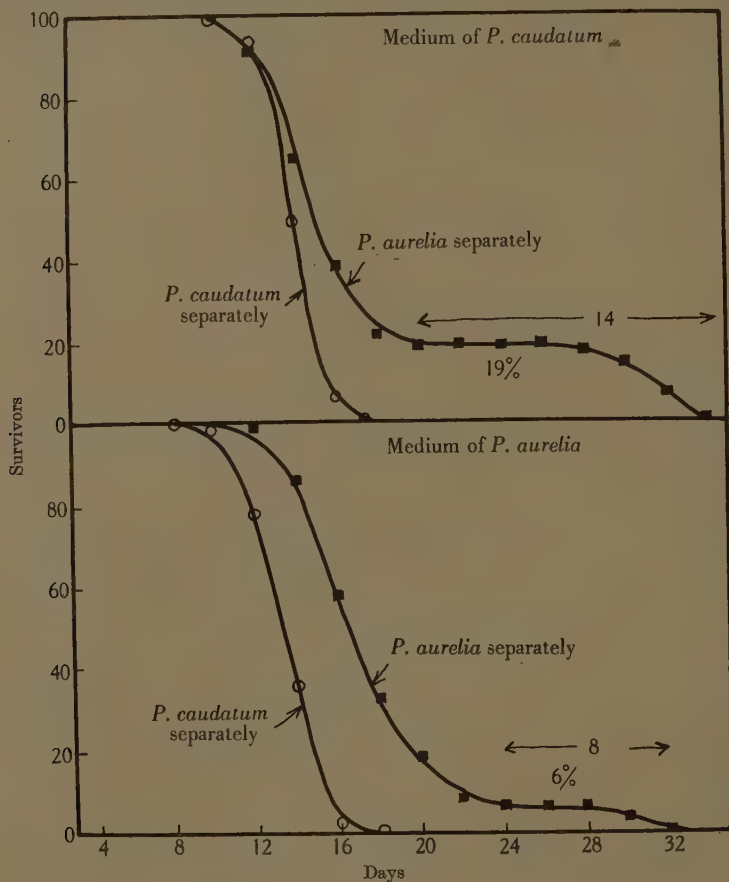


Fig. 5. The relative curves of decline of *P. caudatum* and *P. aurelia* in pure populations.

for 100 in all the cases, and the corresponding relative curves of decline may be found in Figs. 5 and 6.

The analysis of the curves of decline shows the existence of an essential difference between *P. caudatum* and *P. aurelia*. The population of *P. caudatum* dies out rapidly and disappears entirely on the eighteenth day. The rate of

the decline varies of course under different conditions, but these differences are small. Another state of affairs is found in *P. aurelia*. When about 90 per cent. of the population has already perished, the remainder (the experiments were made with pure cultures!) adapt themselves to the rather unfavourable

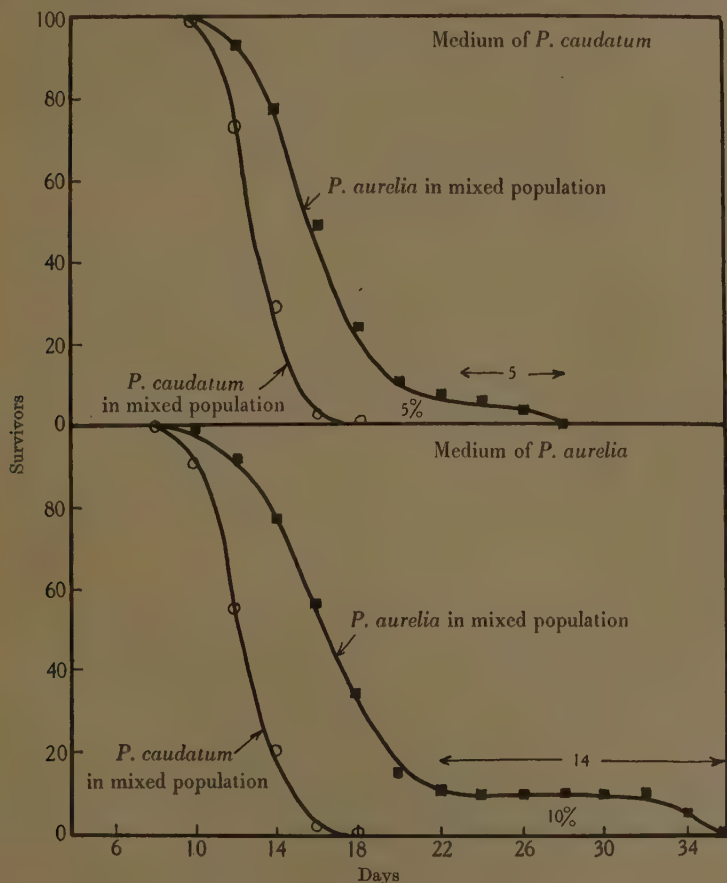


Fig. 6. The relative curves of decline of *P. caudatum* and *P. aurelia* in mixed populations.

conditions and continue to live for a certain time. Later there appears a second cycle of decline sharply separated from the first. The second cycle of decline in *P. aurelia* presents an extraordinary sensitiveness to the homotypic and heterotypic conditioning of the medium:

(1) *P. aurelia* in pure culture on a "homotypic" medium possess a relatively lower level of the second cycle than on a "heterotypic" one (6 per cent.

as compared to 19 per cent., Fig. 5), and it is of shorter duration (8 days instead of 14). The level is here taken in a relative form and is apparently not connected with the lower absolute values of growth on the *P. aurelia* medium. It seems that here the waste products of the species itself are more toxic than those of the other species.

(2) If *P. aurelia* grows on the unfavourable "homotypic" medium, but in presence of *P. caudatum*, the second cycle of decline of *P. aurelia* appears to be more powerful than in a pure culture on the same medium. (The level 10 per cent. as compared to 6 per cent., and the duration of 14 days as compared to 8.) This observation demonstrates directly the weaker toxicity of the heterotypic conditioning for *P. aurelia*.

V. CONCLUSION.

Returning to the problem of the relative adaptation of two species at different stages of population growth we can conclude that *P. caudatum* under the conditions of our experiments has an advantage over *P. aurelia* in the coefficients of geometric increase, whilst *P. aurelia* surpasses *P. caudatum* in its resistance to waste products. (This finds its expression in the values of the coefficients of the struggle for existence and in the presence of two cycles in the dying out of the population.) Therefore, if the decisive factor of competition is a rapid utilisation of the food resources, *P. caudatum* has an advantage over *P. aurelia*; but if the resistance to waste products is the essential point, then *P. aurelia* will take the place of *P. caudatum*.

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PERIODIC FLUCTUATIONS IN BRITISH GAME POPULATIONS

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(*With thirteen Figures in the Text.*)

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I. INTRODUCTION.

THIS work forms part of a programme of research on British game populations carried on by the Oxford University Bureau of Animal Population with the aid of a grant from Imperial Chemical Industries. Work of this kind is necessarily dependent a great deal on the degree of co-operation obtained from landowners, shooting men and gamekeepers on private estates throughout the country. I wish to thank all those who have readily placed their game records at my disposal and given me help and facilities for research in many ways. Many landowners do not like to have their names or the names of their estates published, so throughout this paper I have referred to estates only by the name of the county with a reference letter where necessary. A number of other records have been obtained, but only a selection of those which cover the longest series of years are published here. The complete records are deposited at the Bureau of Animal Population.

The aim of this paper is simply to record some facts regarding the periodic fluctuations of certain species of mammals and birds for which statistical data are available in Great Britain. All the records given are the numbers of animals killed annually on game preserves in different parts of the country, and it is as well to say at the outset that most of these figures cannot be regarded as accurate annual indices of the populations concerned. The whole purpose of game management is directed towards the preservation and main-

tenance at a high density of a few species, with as complete a suppression of predatory species as possible, while a heavy annual toll is taken in the shooting for sport of the preserved species. It is impossible, therefore, to be certain that these records are a true reflection of the fluctuations game animals would be subject to under conditions where all species are free from human interference. On the other hand, it may be argued that with many of the game species the proportion of the population killed by man approximates to the reduction by predators under natural conditions. In the more efficiently managed game preserves, however, other practices are carried out in favour of the maintenance of a high game population as well as the reduction of predatory animals. None of the populations here dealt with is appreciably influenced by restocking or the rearing of additional numbers in captivity—as with pheasant management—although Hungarian partridges or their eggs have frequently been introduced in small numbers on to some estates in order to increase the native partridge population.

In order to show more clearly the important periodic fluctuations the figures have been smoothed for the purposes of graphs in this paper, the figure for each year being taken as the mean of three $\left(\frac{a+b+c}{3}\right)$. All the original (unsmoothed) figures on which the graphs are based are given in tabular form at the end of the paper.

II. RABBITS AND HARES.

In Figs. 1–6 several series of records of the numbers of rabbits (*Oryctolagus cuniculus*) and hares (*Lepus europaeus*) killed annually on various estates are shown graphically. The periods covered by these and the records for other species will be seen to vary considerably on different estates owing to the fact that old game books are not always preserved when estates change hands, or to other unavoidable circumstances which make it impossible to obtain a long and continuous record for each estate. Fig. 1 is a graph of the numbers of rabbits killed on a large estate in the north of England, Yorkshire (a), and includes all those killed by the owner and his employees. Fig. 2, for another large estate, Norfolk (a), is based on the numbers killed in the course of normal game shooting, but does not include the very large numbers killed by keepers and trappers. Other graphs of rabbits are given in Fig. 5, Norfolk (b), and Fig. 6, Hertfordshire.

It will be noticed that each of these graphs shows a fluctuation which appears to be periodic. The peak years and the average periodicity for each estate appear to be as follows:

Fig. 1. Yorkshire (a):	1870, 1878, 1884, 1892, 1901, 1910, 1919.	Av. period = 8.5
Fig. 2. Norfolk (a):	1876, 1885, 1891, 1899, 1905, 1911, 1922.	Av. period = 7.7
Fig. 5. Norfolk (b):	1889, 1897, 1904, 1911, 1920, 1928.	Av. period = 7.8
Fig. 6. Hertfordshire:	1905, 1914, 1926.	Av. period = 10.5

The uncertain period before 1885 in Fig. 5 is omitted.

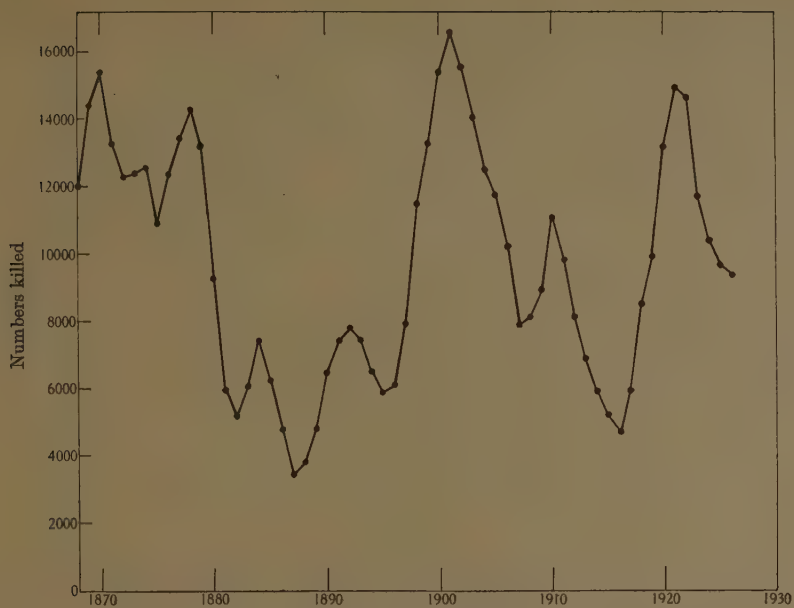


Fig. 1. The numbers of rabbits (*Oryctolagus cuniculus*) killed on Yorkshire (a) estate, 1868-1926.
 (Figures smoothed $\frac{a+b+c}{3}$.)

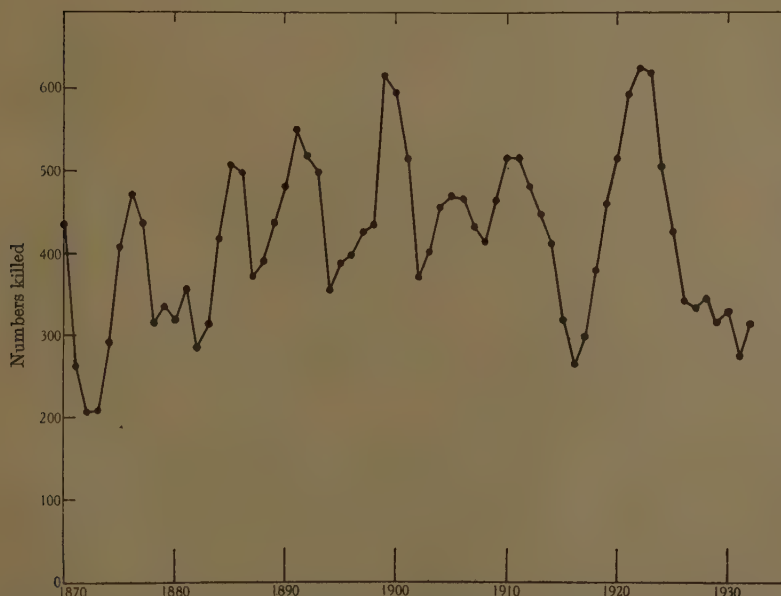


Fig. 2. The numbers of rabbits (*Oryctolagus cuniculus*) killed on Norfolk (a) estate, 1870-1932.
 (Figures smoothed $\frac{a+b+c}{3}$.)

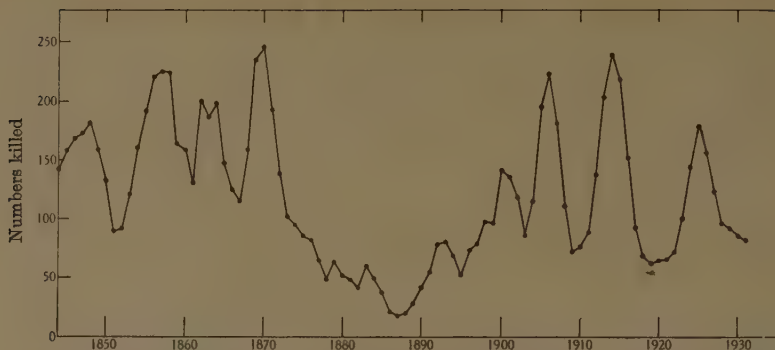


Fig. 3. The numbers of brown hares (*Lepus europaeus*) killed on Yorkshire (b) estate, 1844–1931.

(Figures smoothed $\frac{a+b+c}{3}$.)

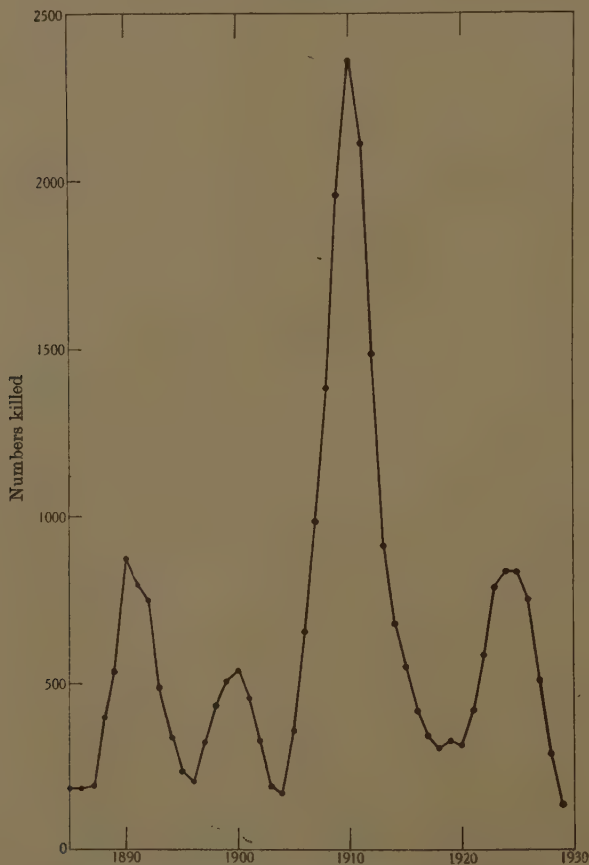


Fig. 4. The numbers of Mountain hares (*Lepus timidus*) killed on Perthshire (a) estate, 1885–1929.

(Figures smoothed $\frac{a+b+c}{3}$.)

This gives a mean periodicity of 8.6 years for the combined records of those four estates. Many of the peaks for each estate obviously synchronise with those of the others, but there is no constant agreement over a long period. It is impossible to make any assumption from these graphs of a regular cycle

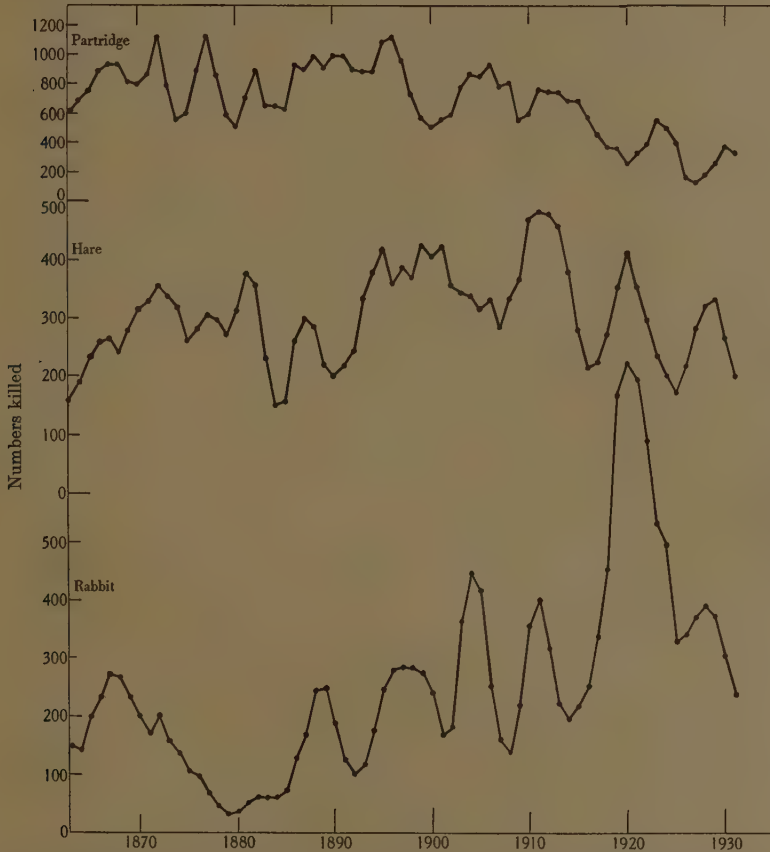


Fig. 5. The numbers of partridges (*Perdix perdix*), hares (*Lepus europaeus*) and rabbits (*Oryctolagus cuniculus*) killed on Norfolk (b) estate, 1863-1931. (Figures smoothed $\frac{a+b+c}{3}$.)

of 8.6 years affecting the rabbit population, and, as records of the numbers killed on different estates form the only data available for the past, it is very difficult to reach any clear conclusion regarding the true significance of the curves. The magnitude of the fluctuations and their periodic occurrence do, however, leave little doubt that an important—probably cyclic—fluctuation is going on, comparable with the cycles found by Elton (1) in snowshoe rabbits

(*Lepus americanus*), *Lynx* (*Lynx canadensis*) and other North American mammals.

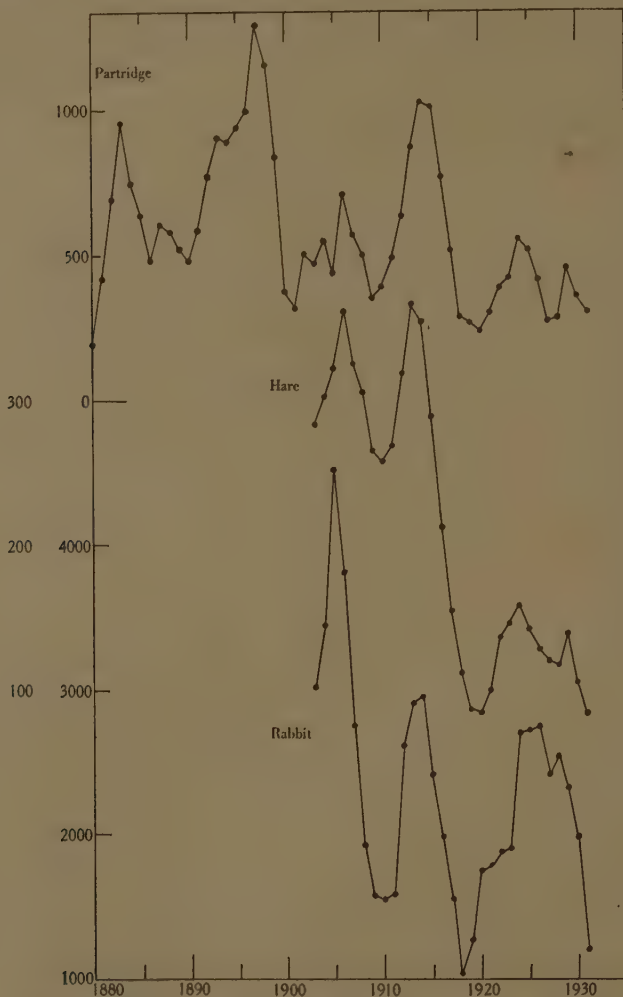
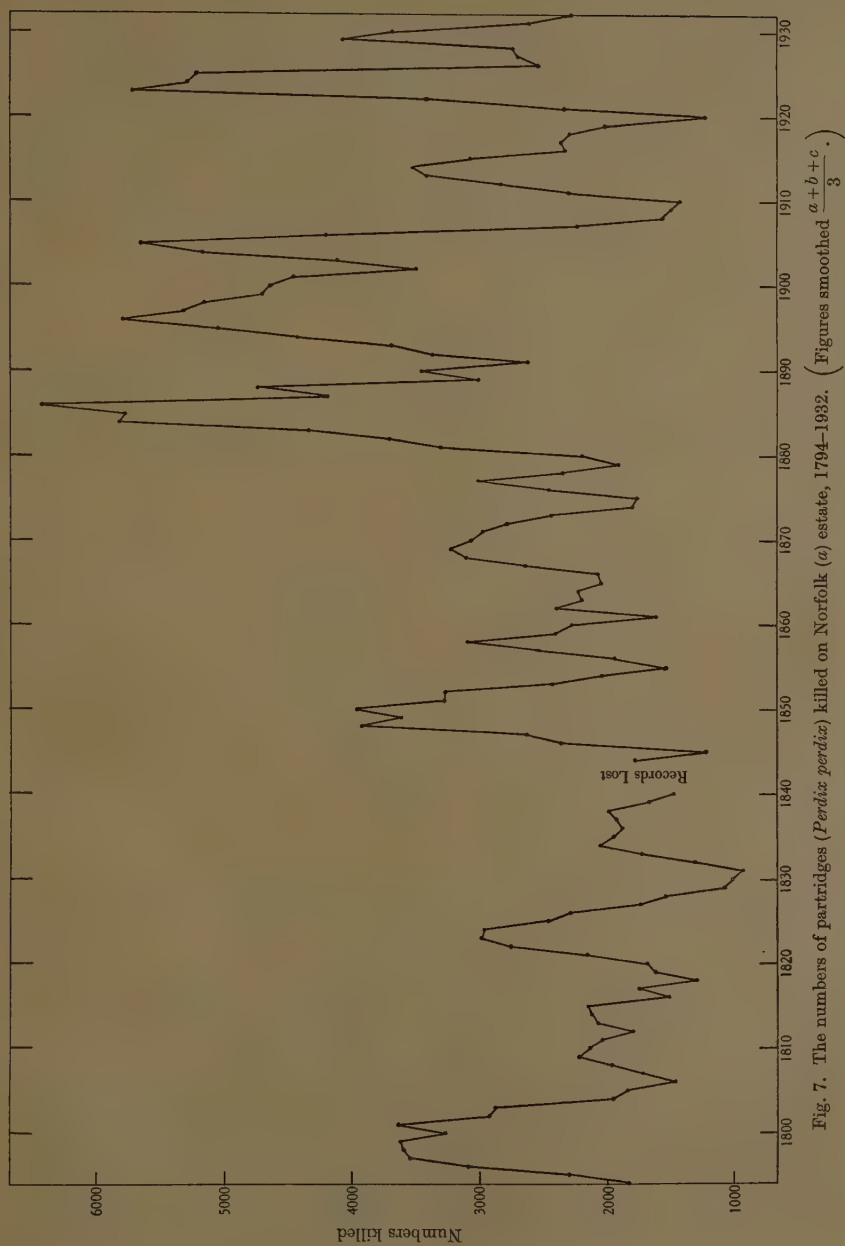


Fig. 6. The numbers of partridges (*Perdix perdix*), hares (*Lepus europaeus*) and rabbits (*Oryctolagus cuniculus*) killed on a Hertfordshire estate, 1880-1931. (Figures smoothed $\frac{a+b+c}{3}$.)

The graphs for brown hares (*Lepus europaeus*) in Figs. 3, 5 and 6 show a very similar fluctuation, and in Figs. 5 and 6 a close agreement between the peaks for rabbits and hares on the same estate is obvious. There does not,



however, seem to be anything except a possible inverse correlation between the two estates Norfolk (*b*) and Hertfordshire, although there appears to be a good deal of agreement between Hertfordshire and Yorkshire (*b*) (Figs. 3 and 6). The peak years are taken to be as follows:

Fig. 5. Norfolk (*b*): 1872, 1877, 1881, 1887, 1895, —, 1911, 1920, 1929. Av. period = 6.8

Fig. 3. Yorkshire (*b*): 1848, 1857, 1864, 1870, —, 1893, 1900, 1906, 1914, 1925. Av. period = 7.7

Fig. 6. Hertfordshire: 1906, 1913, 1924. Av. period = 9.0

The uncertain periods 1895–1907 in Fig. 5 and 1875–90 in Fig. 3 are not included.

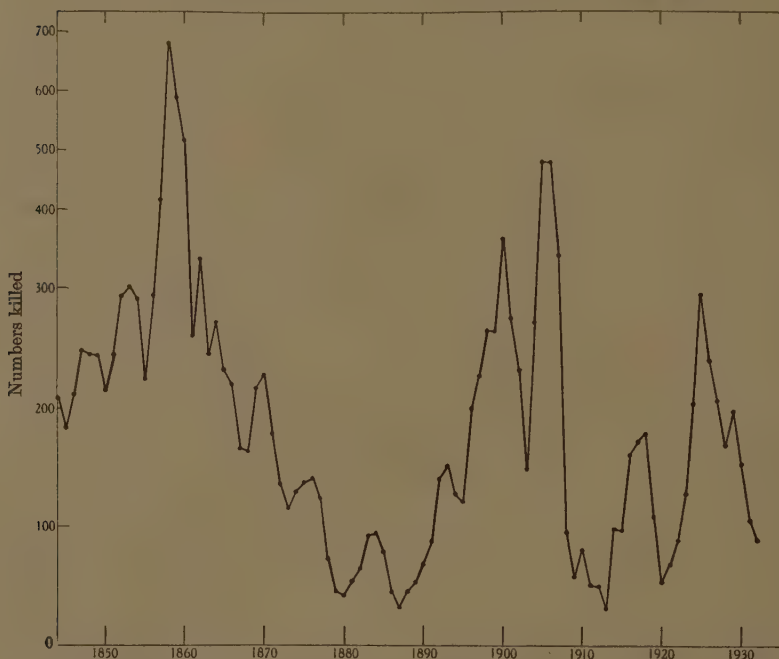


Fig. 8. The numbers of partridges (*Perdix perdix*) killed on Yorkshire (*b*) estate, 1844–1932.

(Figures smoothed $\frac{a+b+c}{3}$.)

This gives an average periodicity of 7.5 years, and there appears to be a general similarity between the rabbit and hare fluctuations.

Fig. 4 is a graph of the fluctuations in mountain (or blue) hares (*Lepus timidus*) on an estate in Scotland, Perthshire (*a*). In the rather short period covered by this curve there is an indication of a pronounced fluctuation with a longer periodicity than that shown by brown hares and rabbits—two 10-year periods and one of 14–15 years. The records for rabbits killed in a neighbouring part of Perthshire (not published in this paper) show no correlation with this curve but have an average periodicity of 8.6 years over 48 years.

III. PARTRIDGES.

Although longer and possibly more accurately kept records are available for partridges (*Perdix perdix*) than for rabbits and hares, the figures are probably not so reliable an index of the population as those for less valuable game species. On all estates from which long records have been obtained, as much as possible is done to preserve the maximum stock of partridges. Keepers take particular care in preserving nests and undoubtedly save large

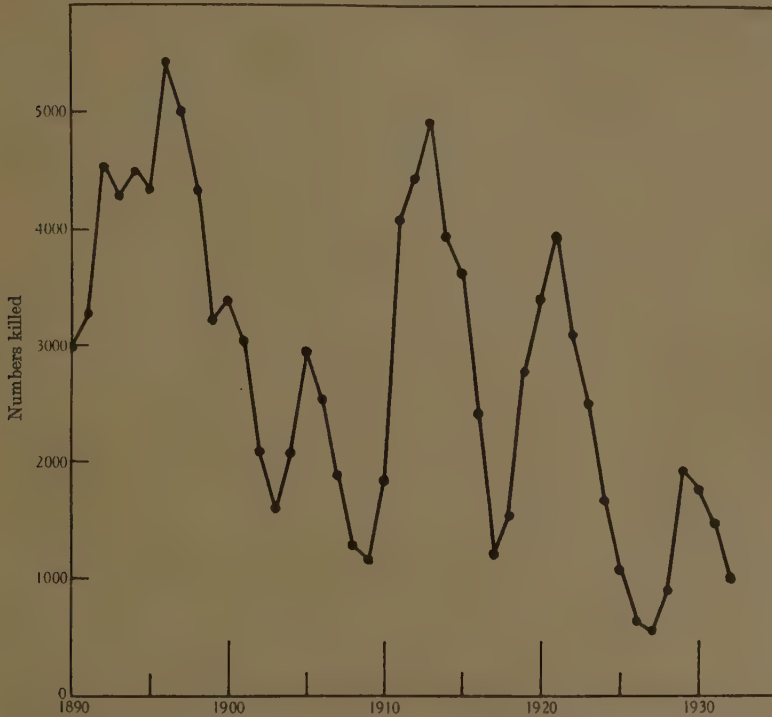


Fig. 9. The numbers of partridges (*Perdix perdix*) killed on a Suffolk estate, 1890-1932.

(Figures smoothed $\frac{a+b+c}{3}$)

numbers of partridges which would not normally survive. Shooting is also controlled on most estates with the object of leaving a large stock for breeding purposes, fewer being shot in "low" years and as many as possible in "high" years: thus one cannot say that the number killed each year approaches a constant proportion of the total population. In spite of all these sources of error, the graphs in Figs. 5-9 do show distinctly periodic features similar to

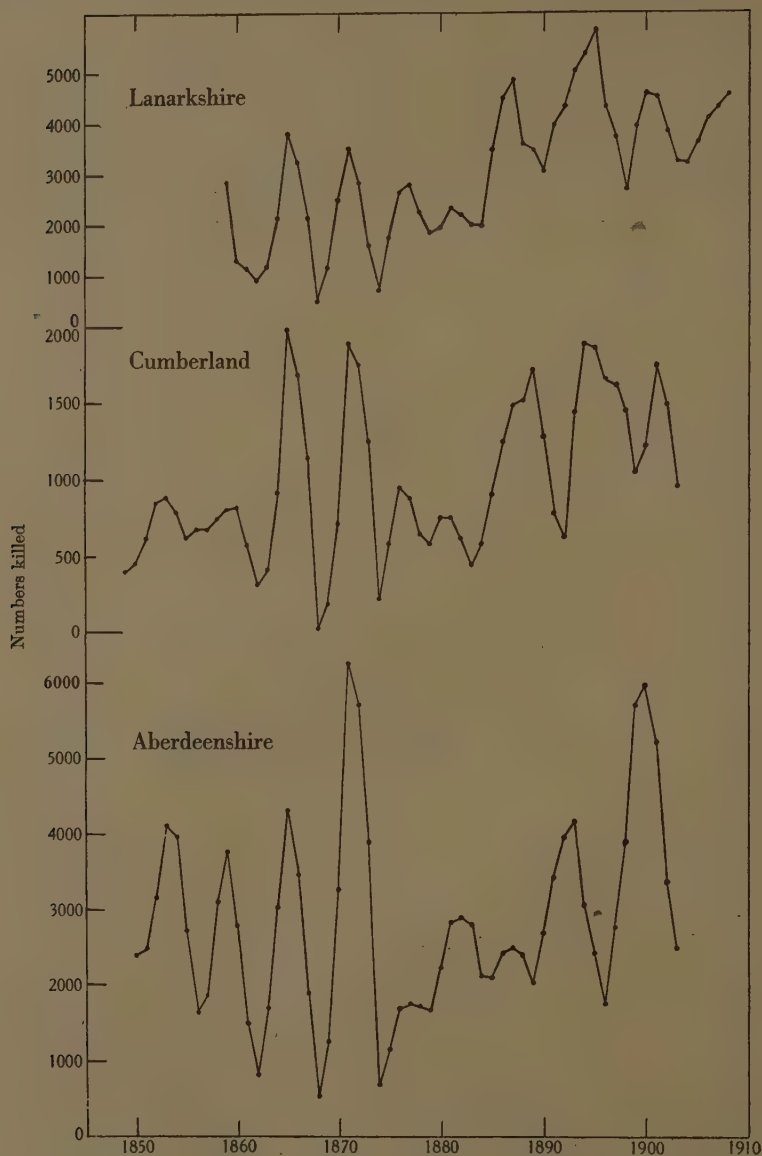


Fig. 10. The numbers of grouse (*Lagopus scoticus*) killed on three different estates in Scotland and England, 1849-1908. (Figures smoothed $\frac{a+b+c}{3}$.)

those of the rabbits and hares. The peak years on the different estates are taken to be as follows:

Fig. 5. Norfolk (b): 1872, 1877, 1882, —, 1896, 1906, 1911, 1923, 1930. Av. period = 7.3

Fig. 6. Hertfordshire: 1883, 1897, 1906, 1914, 1924, 1929. Av. period = 9.2

Fig. 7. Norfolk (a): 1850, 1853, 1869, 1877, 1886, 1895, 1905, 1914, 1923, 1929. Av. period = 8.8

Fig. 8. Yorkshire (b): 1847, 1853, 1858, 1870, 1876, 1884, 1893, 1900, 1906, 1918, 1925. Av. period = 7.8

Fig. 9. Suffolk: 1896, 1905, 1913, 1921, 1929. Av. period = 8.3

The uncertain period 1882–1896 in Fig. 5 is not counted.

This gives a mean periodicity of 8.2 years, which agrees fairly closely with the figures of 8.6 and 7.5 for rabbits and hares respectively. With the partridges there seems to be a definite correlation between the peak periods on different estates, those in Figs. 5, 6, 7 and 9 (estates in Norfolk, Suffolk and Hertfordshire) falling into line with some degree of regularity, but Fig. 8 (North Yorkshire) does not show any such correlation with these. On the Hertfordshire estate (Fig. 6), partridges, hares and rabbits synchronise very closely during the comparatively short period covered by the graph.

IV. GROUSE.

In Fig. 10 are graphs of red grouse (*Lagopus scoticus*) killed on three separate moorland areas in northern England, southern Scotland, and northern Scotland. It will be seen that there is a well-marked periodic fluctuation with agreement between most of the peaks of all three graphs. The periodicity here is obviously shorter than that shown by rabbits, hares and partridges. The peaks for each graph, with their averages, are as follows:

Lanarkshire: 1865, 1871, 1877, 1881, 1887, 1895, 1900. Av. period = 5.8

Cumberland: 1853, 1859, 1865, 1871, 1876, 1881, 1889, 1894, 1901. Av. period = 6.0

Aberdeenshire: 1853, 1859, 1865, 1871, 1877, 1882, 1887, 1893, 1900. Av. period = 5.9

The shorter period (averaging 5.9 years) suggests a different controlling factor from that influencing partridges, rabbits and hares.

In Fig. 11 the records of grouse, blackgame (*Tetrao tetrix*), and partridges killed on the Island of Bute are shown (2). There is no indication here of any agreement with the grouse records for the other three areas, but

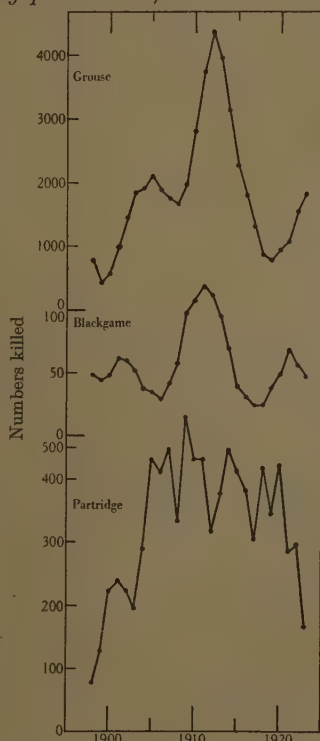


Fig. 11.

Fig. 11. The numbers of grouse (*Lagopus scoticus*), blackgame (*Tetrao tetrix*) and partridges (*Perdix perdix*) killed on the island of Bute (West Scotland) 1898–1923. (Figures smoothed $\frac{a+b+c}{3}$.)

both grouse and blackgame appear to be fluctuating over a longer period. The partridges show no signs of the 8-year period prevalent in England, although there is a suggestion of a much shorter periodicity in this graph.

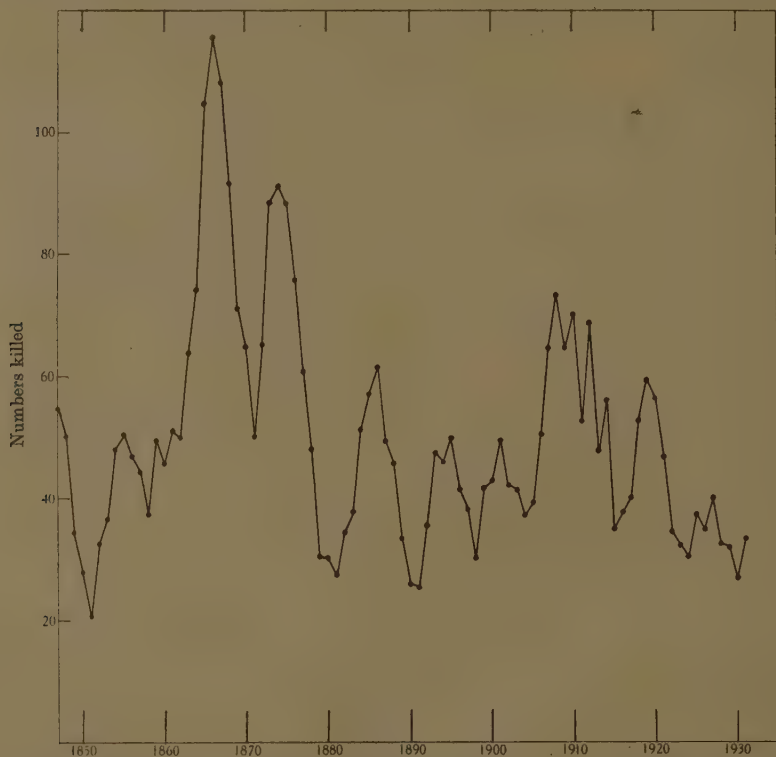


Fig. 12. The numbers of woodcock (*Scolopax rusticola*) killed on an estate in Sussex, 1847-1931.
(Figures smoothed $\frac{a+b+c}{3}$.)

V. OTHER SPECIES.

Fig. 12 gives a graph showing the fluctuations in the number of woodcock (*Scolopax rusticola*) shot on an estate in Sussex. Practically all these birds are killed while on migration in the winter, but the source of the migrants is uncertain. It is generally assumed that they come from Scandinavia, but it is probable that many woodcock killed in Sussex were bred in the north of Great Britain. The fluctuation appears to be distinctly cyclic with an average periodicity of 9 years if the uncertain period between 1905 and 1915 is counted as representing one peak; if there were really two peaks in this period

the average would be 8 years—in any case it corresponds closely with the partridge, rabbit and hare periodicity, although there is no sign of agreement between the peak years for woodcock and the resident species.

The graphs in Fig. 13 form an example of a fluctuation in a carnivore population, although it is most probable that the weasel (*Mustela vulgaris*) is mainly dependent upon mice, voles and young rabbits, and its reaction to fluctuations in game animals would not be very noticeable. The average

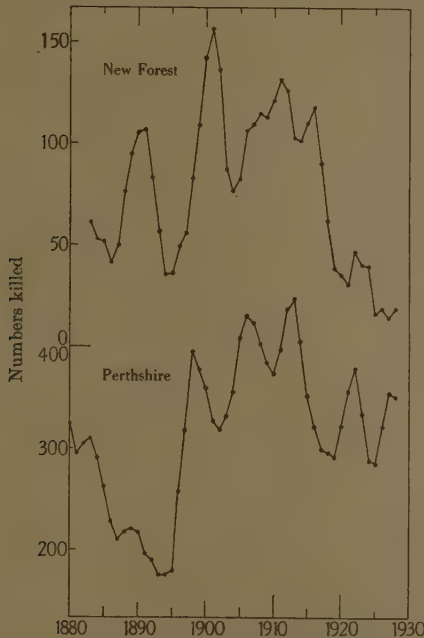


Fig. 13. The numbers of weasels (*Mustela vulgaris*) killed on Perthshire (b) estate and in the New Forest, Hampshire. (Figures smoothed $\frac{a+b+c}{3}$.)

periodicity shown in these graphs appears to be 7.7 years, similar to that for partridges, hares and rabbits, but not resembling the grouse periodicity. The data are, however, too limited to show whether any correlation exists between the weasels and the game species.

VI. DISCUSSION.

It is not proposed to enter into a discussion on the causes of these periodic fluctuations in game animals, since there are insufficient data available at present to make conclusions possible. It seems reasonable to assume that these pronounced fluctuations must be due to some natural factors outside

the practice of game management, since every effort is directed towards maintaining a stable though high density, and there is little reason to suspect that any agricultural or man-controlled practices would be the cause. The more regular cycles in numbers of North American animals or Scandinavian lemmings, for example, are most obvious in populations which have little contact with man, and it is most likely that man's activities tend to mask any natural cycles among animal populations. This view is supported by the fact that grouse, whose environment is the least subject to man's interference, show a more definitely cyclic fluctuation than any of the other British game animals. No regular fluctuations have been found in the simple climatic factors such as rainfall, temperature or pressure which show any constant correlation with the records for the animals. The most fruitful line of enquiry may be a study of the effects of different types of radiation and their qualitative fluctuations, acting either directly on the animals or indirectly through plants. It is, however, extremely difficult to get any data for long periods in the past which would be likely to show such fluctuations if they exist.

The mechanism controlling these fluctuations is extremely difficult to trace, since, for example, so many complex factors can and do exert an important influence on the increase or decrease of the population of partridges. Most of these factors can be grouped under the main headings of (1) weather, (2) disease and natural enemies, (3) agriculture and human interference.

Of these the first and last are the more complex and interconnected, and their influence is almost impossible to measure in relation to past fluctuations, although it is hoped that more accurate data will be accumulated in the future. Disease is an important factor in periodically reducing all the native game populations in this country, and there is room for a lot of fruitful research on this subject. The grouse disease, strongylosis, caused by the parasitic nematode *Trichostrongylus pergracilis*, has received a good deal of attention (3), and its periodic occurrence in epidemic form appears to be the normal cause of reduction in numbers on most grouse moors after a peak year. More recently evidence has been obtained of a heavy mortality in partridges after a peak year being due to a closely allied worm, *T. tenuis* (4).

In conclusion it may be said that, although it is now difficult to interpret the true significance of the old game records dealt with in this paper, the fluctuations shown appear of sufficient scientific interest and practical importance to warrant a more careful compilation of data in the future. This is now being done by getting censuses, fertility records, etc., on several representative estates and by a study of the factors influencing game populations.

VII. SUMMARY.

Graphs of the numbers of several British game animals and birds are shown, with the object of demonstrating the periodic fluctuations that have occurred during the past 100 years. There are indications of a periodicity averaging approximately 8 years in the numbers of rabbits (*Oryctolagus cuniculus*), hares (*Lepus europaeus*), and partridges (*Perdix perdix*), and one of approximately 6 years in the numbers of grouse (*Lagopus scoticus*). Graphs are also given of the fluctuations in numbers of mountain hares (*Lepus timidus*), blackgame (*Tetrao tetrix*), woodcock (*Scolopax rusticola*) and weasels (*Mustela vulgaris*), which also show marked fluctuations of a periodic nature.

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APPENDIX.

RECORDS OF THE VARIOUS ANIMALS KILLED ANNUALLY ON DIFFERENT ESTATES
IN GREAT BRITAIN, ON WHICH THE GRAPHS IN THIS PAPER ARE BASED.

Rabbits (Oryctolagus cuniculus) killed on four estates.

Year	Yorkshire (a)	Norfolk (a)	Norfolk (b)	Year	Yorkshire (a)	Norfolk (a)	Norfolk (b)	Hertford- shire
1862	—	—	194	1898	9,717	370	306	—
1863	—	—	124	1899	16,456	542	304	—
1864	—	—	111	1900	13,846	941	260	—
1865	—	—	193	1901	16,222	309	148	—
1866	—	—	287	1902	16,407	305	88	3607
1867	11,615	—	210	1903	17,187	513	293	1428
1868	7,201	—	314	1904	13,359	404	707	3986
1869	17,270	723	273	1905	12,038	464	324	4916
1870	19,197	426	106	1906	12,342	566	208	4667
1871	10,210	166	218	1907	10,867	386	218	1822
1872	10,665	189	182	1908	7,761	351	46	1760
1873	16,072	268	196	1909	5,122	520	137	2190
1874	10,424	167	94	1910	11,667	529	466	793
1875	11,388	435	122	1911	10,265	518	466	1653
1876	11,185	646	45	1912	11,274	516	264	2332
1877	14,910	332	60	1913	8,082	418	221	3869
1878	14,308	336	41	1914	5,191	417	179	2548
1879	13,851	284	24	1915	7,683	391	175	2426
1880	9,161	397	20	1916	4,993	167	283	2259
1881	4,989	275	44	1917	3,029	246	288	1296
1882	3,925	396	64	1918	6,524	497	431	1088
1883	6,918	193	40	1919	8,234	410	648	587
1884	7,373	364	42	1920	10,858	484	1218	2130
1885	8,263	710	66	1921	10,616	666	709	2515
1886	3,131	463	46	1922	17,878	631	420	663
1887	3,161	330	204	1923	16,445	580	681	2437
1888	4,236	331	235	1924	9,709	648	289	2599
1889	4,106	519	289	1925	9,027	287	315	3139
1890	6,095	474	205	1926	13,137	351	317	2368
1891	9,353	452	65	1927	7,648	372	376	2740
1892	7,024	730	96	1928	8,054	279	418	2147
1893	7,250	396	85	1929	—	375	370	2812
1894	8,132	383	122	1930	—	293	322	1998
1895	4,118	287	296	1931	—	318	221	888
1896	5,615	505	305	1932	—	220	163	743
1897	8,486	408	280	1933	—	406	—	—

*Hares (Lepus europaeus) killed on three estates. The records for
Perthshire (a) are Mountain hares (Lepus timidus).*

Year	York- shire (b)	Year	York- shire (b)	Norfolk (b)	Perth- shire (a)	Year	York- shire (b)	Norfolk (b)	Perth- shire (a)	Hertford shire
1843	112	1862	123	113	—	1898	49	486	397	—
1844	155	1863	297	205	—	1899	130	326	552	—
1845	159	1864	137	156	—	1900	109	446	569	—
1846	161	1865	161	205	—	1901	182	443	501	—
1847	184	1866	142	334	—	1902	111	365	309	311
1848	173	1867	72	214	—	1903	63	263	176	294
1849	187	1868	131	216	—	1904	80	393	95	245
1850	118	1869	276	302	—	1905	200	353	230	370
1851	92	1870	297	309	—	1906	309	198	748	349
1852	58	1871	165	326	—	1907	161	430	975	376
1853	124	1872	116	353	—	1908	74	222	1200	247
1854	179	1873	134	377	—	1909	95	345	1985	290
1855	181	1874	52	272	—	1910	46	532	2701	258
1856	212	1875	100	296	—	1911	87	525	2400	224
1857	269	1876	100	205	—	1912	132	387	1237	325
1858	195	1877	41	333	—	1913	194	518	832	410
1859	209	1878	52	371	—	1914	283	464	672	375
1860	88	1879	53	181	—	1915	240	143	537	276
1861	180	1880	85	259	—	1916	132	224	437	216
		1881	18	489	—	1917	80	244	280	147
		1882	45	364	—	1918	64	176	310	102
		1883	60	217	—	1919	60	389	317	86
		1884	74	108	268	1920	62	485	370	71
		1885	15	118	182	1921	71	351	250	102
		1886	22	237	116	1922	63	217	649	126
		1887	25	415	259	1923	80	320	853	184
		1888	6	244	208	1924	156	156	840	127
		1889	26	199	726	1925	195	118	812	181
		1890	54	200	678	1926	183	220	846	120
		1891	45	199	1216	1927	90	295	600	81
		1892	63	253	503	1928	95	329	110	160
		1893	125	268	521	1929	102	330	150	114
		1894	48	472	444	1930	78	321	150	151
		1895	33	396	50	1931	78	131	—	53
		1896	74	376	215	1932	91	141	—	46
		1897	113	296	351					

Partridges (Perdix perdix) killed on six estates.

Year	Norfolk	Yorkshire	Norfolk	Hertfordshire	Suffolk	Year	Norfolk	Yorkshire	Norfolk	Hertfordshire	Suffolk	Bucks
	(a)	(b)	(b)	(b)	(b)		(a)	(b)	(b)	(b)	(b)	
1793	1349	2676	204	—	—	1893	4585	233	651	929	5719	—
1794	1433	1844	184	—	—	1894	3733	63	848	747	3423	—
1795	2594	1814	177	—	—	1895	4976	86	1138	1035	4350	—
1796	2814	990	190	—	—	1896	6426	321	1262	1035	5185	45
1797	3800	4185	205	—	—	1897	5061	211	972	1207	6670	7
1798	3965	2135	288	—	—	1898	3566	146	636	1632	3113	181
1799	2895	4880	185	—	—	1899	5893	330	559	630	3148	203
1800	3685	3372	259	—	—	1900	4599	315	480	250	3414	204
1801	3801	3554	202	—	—	1901	3435	403	462	250	3501	204
1802	4036	2897	273	—	—	1902	5333	106	751	428	2224	227
1803	4731	3325	405	—	—	1903	1700	184	556	843	515	148
1804	9431	1031	226	—	—	1904	5286	155	1004	166	2117	213
1805	1320	1392	242	—	—	1905	8512	475	1031	646	3601	513
1806	1236	1806	208	—	—	1906	3165	814	549	532	3095	689
1807	1863	2246	435	—	—	1907	896	133	1193	947	964	78
1808	9024	3400	611	—	—	1908	2026	36	564	228	1726	742
1809	2590	3493	996	—	—	1909	1141	117	611	334	1241	178
1810	2316	210	172	—	—	1910	694	19	453	500	550	338
1811	1748	3150	388	—	541	1911	2388	104	728	350	3786	338
1812	1811	1437	222	—	—	1912	3800	29	1082	615	7906	179
1813	1707	2562	366	—	—	1913	2243	16	393	942	1619	437
1814	2568	2505	150	—	—	1914	4166	50	726	1062	5212	522
1815	1967	1597	290	—	—	1915	4138	229	911	1082	5007	519
1816	1804	1907	249	—	—	1916	882	142	409	902	648	231
1817	1225	2555	112	—	—	1917	1962	242	385	332	1544	395
1818	1711	3308	137	—	—	1918	4177	261	544	345	1410	284
1819	1420	3385	242	—	—	1919	1208	30	351	220	1701	619
1820	1651	279	272	—	—	1920	1794	96	205	253	5207	129
1821	1893	2172	172	—	—	1921	3895	77	353	271	3238	578
1822	2838	3108	63	—	—	1922	4400	92	507	507	2638	161
1823	3410	1873	141	—	—	1923	8237	215	828	352	1413	188
1824	2665	2426	174	—	—	1924	2874	304	159	820	973	—
1825	2769	1874	134	—	—	1925	4379	393	91	393	832	—
1826	1887	1876	162	—	—	1926	4279	447	91	63	135	—
1827	2163	1877	125	—	—	1927	447	48	191	53	135	—
1828	1114	2841	85	—	—	1928	—	203	111	398	807	—
1829	1234	332	8	—	—	1929	—	255	904	400	1732	—
1830	676	2486	43	—	—	1930	—	4434	339	589	3305	—
1831	1074	1881	76	—	—	1931	—	4462	417	202	255	—
1832	954	1882	3665	—	1013	1932	—	2125	70	202	867	—
1833	1773	1883	3754	—	898	1933	—	1947	223	63	1789	—
1834	2343	1884	5689	—	1003	—	—	—	—	—	—	—
1835	1923	1885	8100	—	369	—	—	—	—	—	—	—
1836	1492	1886	3630	—	518	—	—	—	—	—	—	—
1837	2138	1887	7512	—	586	—	—	—	—	—	—	—
1838	1838	1887	1390	—	760	—	—	—	—	—	—	—
1839	2056	1888	1390	—	451	—	—	—	—	—	—	—
1840	1195	1889	5254	—	371	—	—	—	—	—	—	—
1841	1485	1890	945	—	460	—	—	—	—	—	—	—
1842	—	1891	55	—	651	—	—	—	—	—	—	—
1843	—	1892	151	—	759	—	—	—	—	—	—	—
1844	—	2734	133	—	3705	—	—	—	—	—	—	—

*Grouse (Lagopus scoticus) killed on four estates,
and blackgame (Tetrao tetrix) on Bute.*

Year	Cumber- land	Aberdeen- shire	Lanark- shire	Year	Cumber- land	Aberdeen- shire	Lanark- shire	Bute	Bute (Black- game)
1848	346	—	—	1890	1966	2464	4057	—	—
1849	401	2254	—	1891	171	3614	3174	—	—
1850	471	2402	—	1892	213	4191	3904	—	—
1851	505	2534	—	1893	1496	4163	5648	—	—
1852	902	2539	—	1894	2638	4182	5638	—	—
1853	1146	4470	—	1895	1517	857	4908	—	—
1854	644	5286	—	1896	1432	2298	6745	—	—
1855	592	2145	—	1897	2022	2147	1368	1025	59
1856	638	742	—	1898	1409	3773	2983	786	56
1857	782	2060	—	1899	930	5823	3701	303	31
1858	588	2880	920	1900	764	7442	5285	250	44
1859	865	4448	1405	1901	1947	4573	4740	1171	66
1860	954	3910	1377	1902	2523	3591	3660	1511	75
1861	605	0	1286	1903	12	1894	3043	1583	38
1862	160	637	772	1904	351	1943	3140	2418	44
1863	185	1914	812	1905	—	—	3550	1711	30
1864	922	2548	1998	1906	—	—	4060	2071	31
1865	1644	4743	3618	1907	—	—	4627	1826	28
1866	3402	5700	5948	1908	—	—	3969	1269	66
1867	1	0	208	1909	—	—	4604	1827	78
1868	4	0	336	1910	—	—	—	2894	150
1869	15	1600	1049	1911	—	—	—	3577	92
1870	530	2200	2107	1912	—	—	—	4676	114
1871	1621	6000	4370	1913	—	—	—	4860	128
1872	3548	10600	4073	1914	—	—	—	2352	45
1873	89	506	170	1915	—	—	—	2073	35
1874	91	583	549	1916	—	—	—	2296	36
1875	464	990	1482	1917	—	—	—	1021	23
1876	1200	1877	3382	1918	—	—	—	483	17
1877	1144	2233	3060	1919	—	—	—	961	37
1878	314	1189	1740	1920	—	—	—	759	59
1879	472	1827	2162	1921	—	—	—	1023	47
1880	953	2084	1500	1922	—	—	—	1414	95
1881	820	2804	2136	1923	—	—	—	2163	27
1882	464	3672	3316	1924	—	—	—	1836	18
1883	606	2199	1055	1925	—	—	—	—	—
1884	292	2612	1664	1926	—	—	—	—	—
1885	832	1542	3285	1927	—	—	—	—	—
1886	1571	2200	5588	1928	—	—	—	—	—
1887	1324	3600	4439	1929	—	—	—	—	—
1888	1534	1710	4547	1930	—	—	—	—	—
1889	1670	1941	1974						

Woodcock (Scelopax rusticola) killed on a Sussex estate.

Year	No.	Year	No.	Year	No.
1836	6	1861	29	1885	75
1837	24	1862	55	1886	62
1838	38	1863	67	1887	48
1839	21	1864	71	1888	39
1840	55	1865	86	1889	51
1841	54	1866	159	1890	11
1842	34	1867	103	1891	16
1843	38	1868	64	1892	50
1844	65	1869	109	1893	41
1845	—	1870	42	1894	52
1846	49	1871	45	1895	46
1847	65	1872	64	1896	52
1848	51	1873	88	1897	27
1849	36	1874	115	1898	36
1850	17	1875	71	1899	28
1851	32	1876	80	1900	62
1852	14	1877	77	1901	39
1853	53	1878	26	1902	48
1854	44	1879	42	1903	40
1855	49	1880	24	1904	37
1856	60	1881	25	1905	35
1857	33	1882	34	1906	46
1858	41	1883	45	1907	71
1859	39	1884	35	1908	77
1860	70				

Weasels (Mustela vulgaris) killed on two areas.

Year	Perth-shire (b)	New Forest	Year	Perth-shire (b)	New Forest	Year	Perth-shire (b)	New Forest
1879	431	—	1897	393	53	1914	398	74
1880	258	—	1898	360	98	1915	358	128
1881	287	—	1899	431	103	1916	298	131
1882	322	69	1900	341	132	1917	310	100
1883	309	56	1901	305	198	1918	287	42
1884	299	65	1902	335	146	1919	297	45
1885	263	43	1903	319	70	1920	286	32
1886	221	53	1904	336	48	1921	366	30
1887	198	34	1905	410	117	1922	397	33
1888	211	70	1906	487	86	1923	354	78
1889	242	131	1907	394	125	1924	249	11
1890	207	90	1908	397	121	1925	258	31
1891	201	104	1909	419	101	1926	343	9
1892	178	132	1910	339	121	1927	362	17
1893	190	18	1911	363	145	1928	356	19
1894	154	24	1912	488	131	1929	336	21
1895	179	79	1913	459	106	1930	467	—
1896	200	21						

THE DISTRIBUTION OF THE MUSKRAT (*FIBER ZIBETHICUS*) IN THE BRITISH ISLES

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(*With Plates XII and XIII and six Maps in the Text.*)

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I. INTRODUCTION.

THE muskrat, introduced for fur-farming purposes into the British Isles, has escaped and spread from several centres during the last few years, and various measures have been adopted for its control. The campaign of destruction undertaken by the Ministry of Agriculture and Fisheries included a special biological investigation of the ecology of the muskrat, with the object of discovering improved methods of detection and control. The Ministry made a grant to the Bureau of Animal Population, and I was appointed by the Bureau to work for a year in Shropshire. The results of this biological survey have not yet been published, but copies of my report are available in the Bureau of Animal Population at Oxford and at the Ministry of Agriculture and Fisheries in London. The present account of the introduction and spread of the muskrat in the British Isles forms a necessary background to the other work on habitats, numbers, parasites, etc. It has been compiled from various sources, including the weekly time-sheets of trappers, copies of which for Shropshire, Surrey and Sussex are deposited at the Bureau. Information concerning the places where muskrats have been kept, as well as many of

the records of escapes, have been obtained from files in the Ministry of Agriculture and Fisheries and the Department of Agriculture for Scotland, to whom my thanks are due¹.

II. DIFFICULTY OF DETECTION.

Owing to their nocturnal and elusive habits, evidence as to the first appearance of muskrats in an area is often not obtained till they have become common, which may be a year or two after the initial escapes. So-called positive evidence as to the occurrence of the animals is subject to doubt unless a specimen is obtained, or unmistakable signs are found—usually investigation of reports that muskrats have been seen shows that only water voles and brown rats are present.

By the Destructive Imported Animals Act of March 1932 it was made illegal to keep muskrats without a licence. Between April 30th and June 23rd, 1932, fourteen licences were issued to keep muskrats up to April 30th, 1933. Non-licence-holders had either to kill their stock or dispose of them to a licence-holder. In March 1933 an order was issued prohibiting absolutely the import and keeping of muskrats in Great Britain as from April 1st, 1933. Before this order came into force, five licence-holders destroyed eighty-two muskrats in their possession. Similar laws have been passed in the Isle of Man and the Irish Free State. In 1932 and 1933 the Governments concerned organised trapping campaigns in an attempt to exterminate muskrats at large in the following areas: Shrawardine, Shropshire; Farnham, Surrey; Pulborough, Sussex; Feddal, Perthshire; Nenagh, County Tipperary.

III. INTRODUCTION INTO THE BRITISH ISLES.

The great majority of the persons who kept muskrats in the British Isles intended them for fur-farming. In England, the first muskrats known to be imported for this purpose were purchased in May and June 1929, and kept at Shoeburyness. Already in 1929 muskrats had been kept at Great Missenden, Bucks; but the date of first introduction there is unknown. In early summer of 1930 Mr M. A. C. Hinton and Mr E. C. Read investigated the keeping of muskrats for profit in England. Attached to their report is a list of seventy-six people who were keeping or who had kept muskrats (some of these names were, however, only included on hearsay). Many fur farms remained undiscovered and unvisited, and since 1930 the existence of more has come to light; all are probably not yet known. In 1930 the two largest pen establishments in the country were doing a brisk business in supplying potential fur-farmers with stock. Most of the latter worked on a very small scale, possessing only one or two pairs. The report shows that the muskrats were, as a rule, kept in galvanised iron pens, or in natural conditions in pools fenced round. Sometimes the conditions of sanitation and environment were most

¹ I am indebted to Mr T. G. Malthouse for permission to use three photographs taken by him.



Map 1. Places where muskrats have been kept in the British Isles. (The numbers refer to the list in Appendix II.)

unsuitable, and gave the animals every incentive to try to escape. Below is given a table summarising the available information about places where sporadic escapes have been reported. The main well-known centres of establishment are given fuller treatment later on, and are not included in the table.

*List of fur farms from which escapes are known to have taken place,
and sporadic appearances of muskrats in England.*

Beccles, Suffolk.	Escapes probable.
Prestbury, Glos.	Three known to have escaped by summer 1930.
Middleton Cheney, Oxon.	Escapes, but said to be all accounted for.
Great Missenden, Bucks.	Reported escapes in 1929.
Louth, Lincs.	Male shot in Hubbard's Valley near Louth, in July 1930. Two reported seen in April 1931. "House" disturbed in November 1931. Two muskrats escaped in 1929 from a muskrat farm $1\frac{1}{2}$ miles from Louth.
Wharfe Valley, between Harrogate and Otley.	Two escaped in middle of 1931.
Freshfield, near Southport, Lanes.	One reported killed April 1931.
Ainsdale, near Southport, Lanes.	One reported killed December 1931, fur farm formerly at Freshfield.
Reading, Berks.	Run over on Oxford Road near Reading in May 1931, may have originated from either Caversham or Reading, at both of which places muskrats were kept.
Hundridge, Bucks.	Two reported captured, December 11th, 1931.
Great Bramingham, Beds.	One reported captured, December 11th, 1931.
Fulbourne, Gt. Wilbraham, Cambs.	Male killed in ditch, old burrow found, May 1932.
Saul Lodge, Frampton-on-Severn.	Muskrat killed in ditch $\frac{1}{2}$ mile from Severn, June 30th, 1931.
Sharpness, Berkeley.	Dead body of muskrat found in lock, July 1933. Both above animals may have come from original escapes at Prestbury, Cheltenham.
Newquay, Cornwall.	One killed, August 18th, 1933. Muskrats said to have been kept three miles away.
Beachley, Chepstow, Glos.	Male killed on tidal beach, April 23rd, 1934, possibly a migrant from a colony originating from the Prestbury centre.
Purley, Surrey.	Male picked up dead on main Brighton road between Purley and Coulsdon, April 25th, 1934.
Ulcombe, near Maidstone.	One killed October 1932.

IV. THE SHROPSHIRE CENTRE.

The main infested area in England has its centre of origin at Shrawardine, near Shrewsbury. The fur farm here was one of the largest in the country conducted on natural lines: a 40-acre pool, adjoining reed bed and a coppice were enclosed by a chain-mesh fence. The fence at one place ran across a corner of the pool. The muskrats which were liberated in the pool were brought directly from North Rice Lake, Ontario. Of 120 animals landed alive, only eighty or less are estimated to have survived after introduction. The muskrats were released in the enclosure in October 1929 and fifteen lodges were built by the end of the year. The fence must have been inadequate or defective, as muskrats were seen abroad soon after fur-farming had begun. Indeed it seems probable that by the end of 1930 some had found their way to the Severn,

which runs barely half a mile away, and *via* neighbouring ditches to a very swampy area known as the New Pool, $1\frac{1}{2}$ miles away. Certain it is that the apparently sudden appearance of a heavy population of muskrats in Salop in 1931 can only be accounted for by numerous desultory escapes followed by breeding while at large in 1930, by wholesale escapes in 1931, or by both these possibilities acting together. In Shrawardine Pool itself, seventy-five lodges were built in 1930 and over 200 in 1931. In early spring of 1931 several muskrats were seen and trapped on the River Perry near Baschurch. (The Perry joins the Severn 5 miles by river below Shrawardine.) The floods in 1931 showed the commonness of the muskrat: the animals, displaced by the rising water from their burrows in the Severn banks, sheltered in groups in willow bushes and could then be seen during the daytime. By the end of 1931 it is probable that at least 20 miles of the Severn, from Molverley to Shrewsbury, was infested. There is evidence that some at any rate travelled much farther upstream than Molverley, for in February 1933 a muskrat house was found on a pool near Leighton Bridge, Welshpool. This had been built during the winter of 1931-2. Leighton is 20 miles by river above Shrawardine. The marshlands, ditches and pools of hamlets near Shrawardine, on the same side of the river within a semicircle of about $2\frac{1}{2}$ miles radius, were infested. Occupied areas on the other side of the river were much smaller. The muskrats in the fur farm were left unmolested till the winter of 1931-2, when the occupier trapped 870. Towards the end of 1931 the enclosing fence was found to be defective below the waterline, so that the animals could escape and re-enter at will. By 1932 muskrats were so numerous on the infested stretch of the river that they were often seen swimming abroad in the twilight. In February of this year (1932) muskrats were noticed at Linley on the Severn below Ironbridge. Active official measures were taken in June, when a staff of five trappers was appointed. The notes taken by the field supervisor show that by summer 1932 the maximum distribution of the muskrats on the river had nearly been reached. The following tributaries of the Severn entering the infested length also harboured muskrats to a greater or less extent: River Morda, River Vyrnwy, Argoed ditches, River Perry, Rad Brook, Rea Brook, River Tern, as well as many small side ditches.

In November 1932 the staff was increased, and the larger trapping area and the more intensive work then practicable enabled for the first time a reasonably accurate map of distribution to be drawn up. Little change occurred in the status of the muskrat in the first two months of 1933. Catches were very heavy during the spring migration in March, and the infested area increased, though only slightly. The effect on the muskrat population of the Severn of this slight spread was not apparent at once, owing to the time lag in detection of the migrant animals, but, during the next two or three months, stragglers were caught many miles upstream and downstream from the main area. From April to August the muskrat population on ponds and waterways



Photo. G. T. Malthouse

Phot. 1. Feeding-place of Muskrat, *Iris* stems cut off, Shropshire.

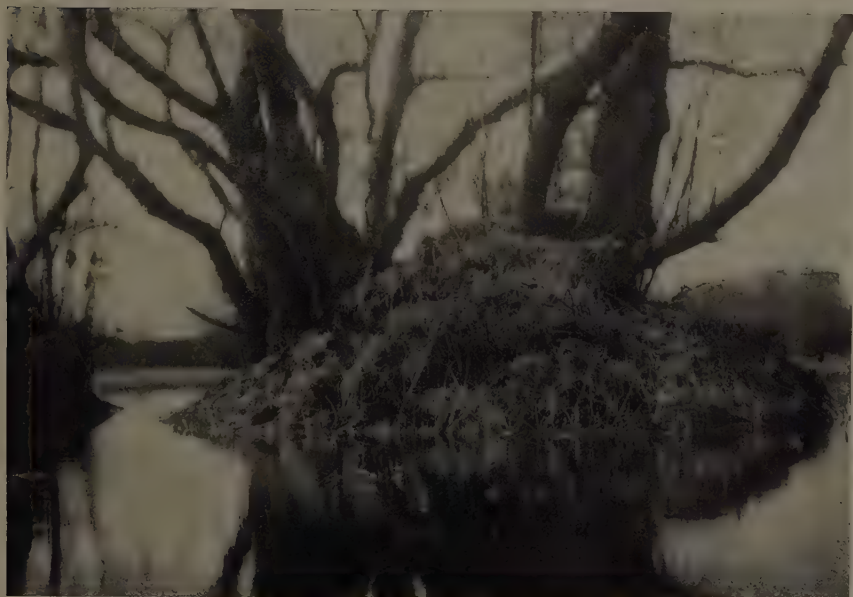
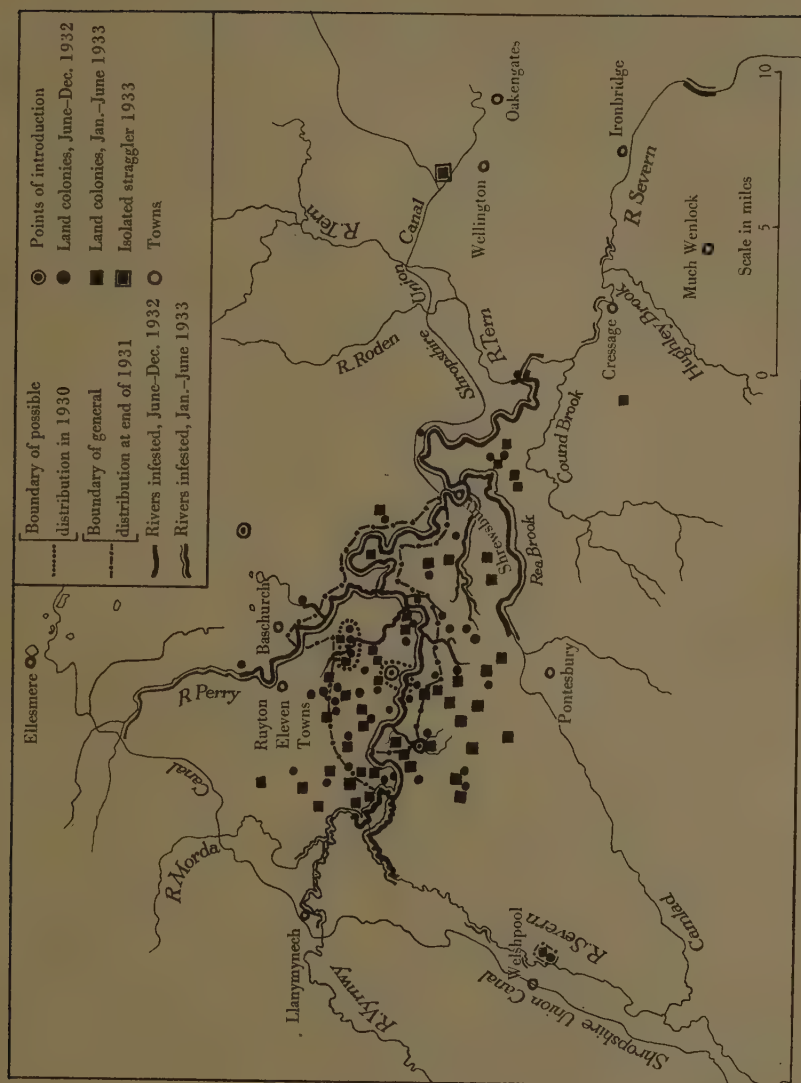


Photo. G. T. Malthouse

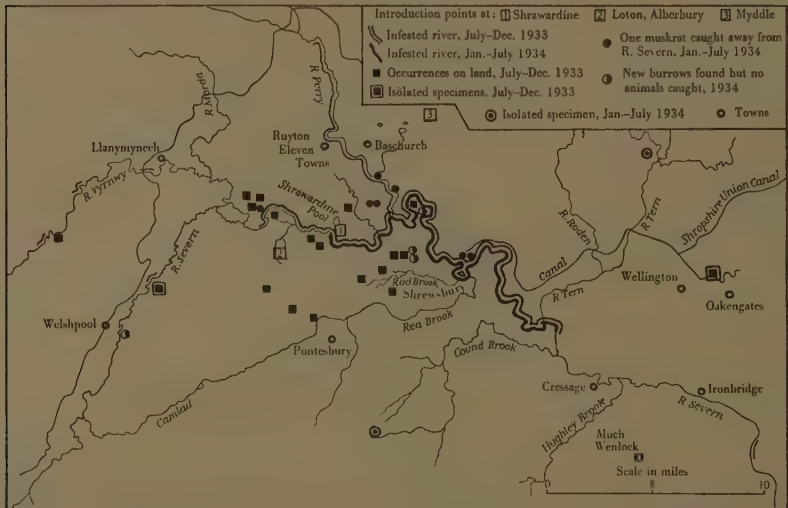
Phot. 2. Large muskrat house, Shrawardine Pool, Shropshire.



Map 2. Distribution of muskrats in Shropshire from chief introduction point at Shrewsbury, Shrewsbury, in 1930, 1931, June–December 1932, and January–June 1933.

apart from the Severn was steadily trapped out, and by the end of the year muskrats were, so far as is known, confined to the Severn. During the migratory season in November catches increased again, but not to the high level of March. At this time a few muskrats left the river and were trapped in pools. During 1933, thirty-three muskrats were caught between Linley and Ironbridge on the Severn, at and below the place where they had first been noticed in February 1932. They were supposed to have been exterminated by the end of the year.

Results of trapping in 1934 show that almost certainly the only muskrats resident in Shropshire now are those living on the Severn. No muskrats have been caught above Shrawardine, though there is evidence that this part of



Map 3. Distribution of muskrats in England in the Shrewsbury area, July-December 1933 and January-July 1934.

the river has been used by wandering animals. Though the total infested length has thus been reduced, its lower limit remains approximately the same, at Wroxeter. After the Severn had been superficially searched from Shrewsbury to Gloucester, a male muskrat was caught near Bewdley on June 26th, 1934. This is the lowest point on the Severn at which a muskrat has been trapped.

Viewed as a whole the area formerly infested in Salop was compact. This was probably owing to the proximity of the point of infestation both to a highly suitable river, and to the presence of many ditches and small pools. At the height of infestation, the Severn was colonised for 9 miles above and 27 miles below Shrawardine. Between this lower limit and the outpost still further downstream at Linley very few muskrats have been caught.

Conditions in the Severn are very favourable for muskrats. The river contains a great deal of waterweeds, by far the commonest species being *Ranunculus fluitans*. The muskrat can support itself on these succulent food-stuffs and when not migrating need not (and rarely does) show its presence on the sides. The banks are generally quite steep and more or less clayey, and in many places are fringed with willows, under the roots and overhanging ledges of which most of the burrows are made. These conditions mean that detection and trapping are often very difficult, and sometimes physically impossible. Muskrats are proving especially hard to eradicate on the stretch of the Severn 8 to 3 miles above Shrewsbury by river.

Muskrats were kept on a small scale at Loton Park near Shrewsbury and escaped early in 1930. They may have contributed to the infestation of the Severn above Shrawardine.

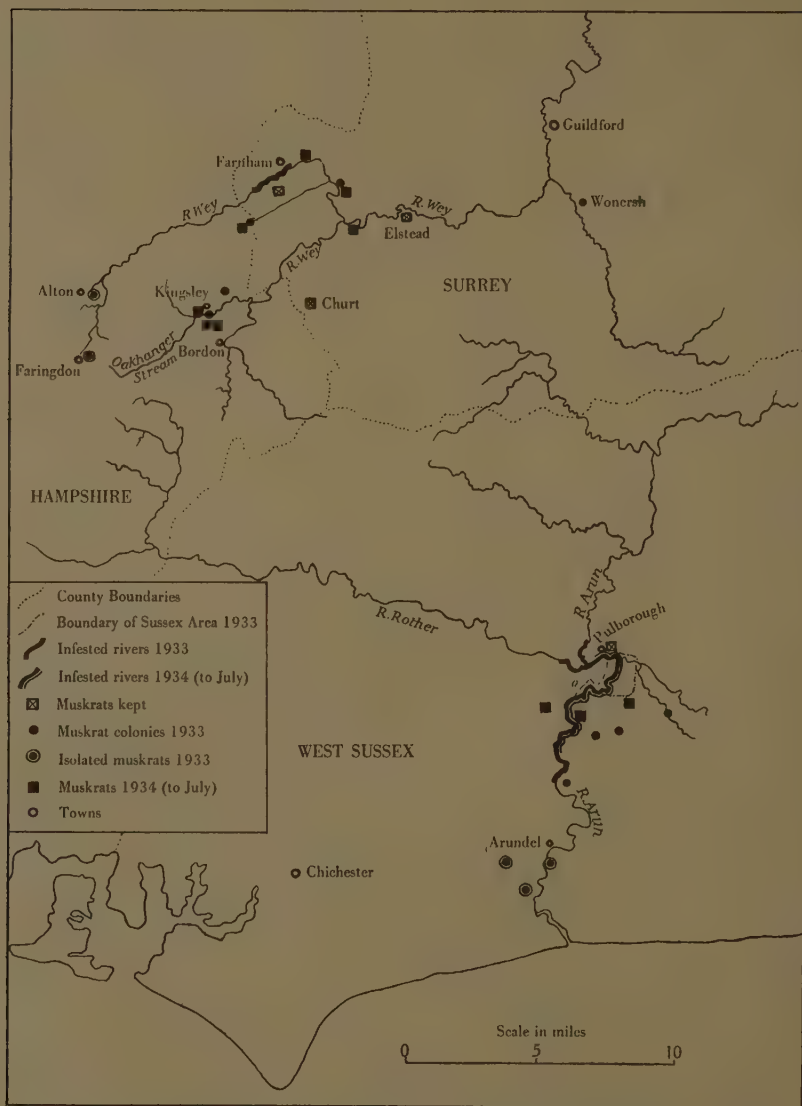
Records of rats sporadically killed away from the main area in Shropshire.

	Approximate no. of miles travelled
Male. Shropshire Union Canal at Leegomery, near Oakengates, 1933	13.5
Male. Shropshire Union Canal at Humbers Arm, October 1933	15
Male. Whitchurch, April 22nd, 1933	20
Male. Coldhatton, April 20th, 1934	11
? Picklescott, Smethcott, July 1934	16

V. THE FARNHAM CENTRE.

Muskrats were kept on the pen-system at Wrecclesham, near Farnham, Surrey. Some are thought to have escaped in 1930 and 1931, and in May 1933 a trapping campaign was begun. On escaping from the fur farm muskrats apparently made use of a nearby ditch, the Bourne, and travelled along to its mouth in the north branch of the River Wey, and to its source at the Lodge Pond, Alice Holt. Two miles of the Wey immediately above Farnham were infested and yielded 50 per cent. of the muskrats caught in the area. Isolated muskrats have been caught downstream a distance of $2\frac{1}{2}$ miles to Waverley, where on a swamp on Moorpark very close to the river ten houses were built in the winter of 1933-4. Stragglers during the spring migration in 1933 travelled from Farnham upstream along the North Wey, one was killed at Alton on April 24th, and another at Faringdon in the same month.

In July 1933 muskrats were reported from a very small pond at Kingsley, Hants; five were trapped here. From September 1933 to February 1934, muskrats were obtained from two very suitable ponds near Bordon Camp. The above two infestations arose from migrant muskrats which had probably travelled from Farnham along the South Wey. No muskrats have actually been trapped on this part of the Wey, though there has been a slight infestation (probably a secondary one) on the Oakhanger Stream, a tributary of the South Wey, near Kingsley. In 1934, twelve muskrats were caught at



Map 4. Distribution of muskrats in Sussex, Surrey and Hampshire.

Moorpark Swamp, Bordon Camp ponds and Oakhanger Stream, as well as an isolated specimen on the Wey at Farnham.

In June 1932, a muskrat was shot at Wonerh Park near Guildford, Surrey, and, as none have been reported there since, it may be presumed that this specimen was a straggler, which had left the main colony in the Farnham area in the spring migration of that year. Burrows have also been found on a side ditch 1 mile below the junction of the north and south branches of the Wey. The main centre of infestation on the Wey at Farnham has been cleared so far as is known, and it is probable that what few muskrats are abroad are scattered. The infestation here was never serious as regards numbers of animals.

At Farnham there is no network of ditches or extensive marshy area to provide harbourage for an extensive muskrat population. This may account for the rather isolated outpost near Kingsley. The River Wey itself provides ample food for muskrats, as it has rank vegetation on its banks as well as aquatic plants on its bed. Trapping presents few difficulties in this area. Muskrats were also kept at Churt and Elstead, Surrey. So far as is known they did not contribute to the infestation. Only one animal was kept at the latter place.

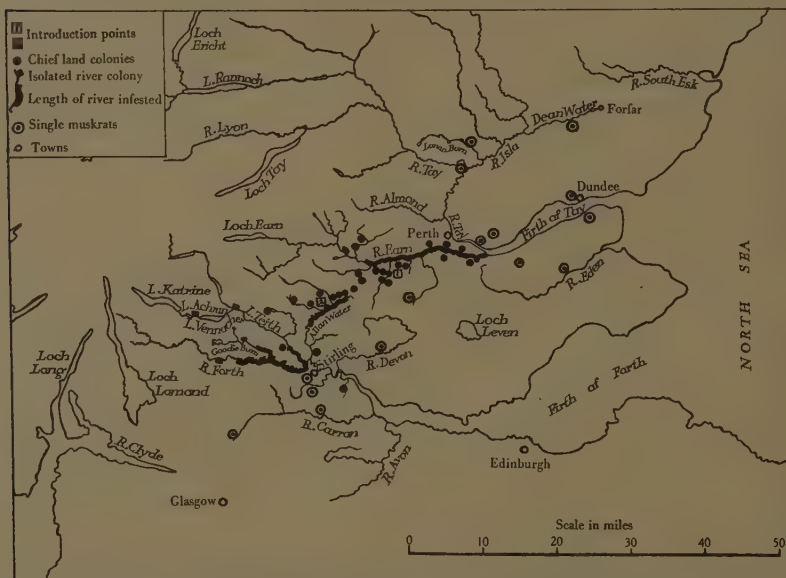
VI. WEST SUSSEX.

Muskrats were kept at Pulborough in an artificial pond, and so far as is known no special precautions were made to prevent their escape. The date of escape is unknown, but was probably 1930-1, as by the end of 1932 there was a dense population of muskrats in the neighbourhood. In March 1933 trapping was begun. The infested length on the River Arun extended from 2 miles above Pulborough to 8 miles below. The River Rother was infested for 2 miles above its junction with the Arun. Marshes and ditches on both sides of the Arun for 3 miles below Pulborough were also heavily infested. A small number of isolated muskrats have been obtained on side ditches and streams mainly downstream from the central infested area. A solitary muskrat was obtained on a ditch at Arundel and another near Ford, only 3 miles from the mouth of the Arun by river.

There are quite possibly small numbers of muskrats living in some of the marshes and ditches. The Arun between Pulborough and Amberley is still infested, with most of the muskrats at Greatham. The West Sussex area of infestation is a compact one, largely owing to the fact that immediately south of Pulborough there is an extensive area of marshy ground drained by a ditch system. The muskrats tenanted this at once, but little invasion of similar and equally suitable habitats further downstream took place. Conditions for trapping here are much more difficult than at Farnham, where there are many miles of ditches and much marshy land. Moreover, the entire stretch of river infested is tidal. There is a tide of about 1 ft. at Pulborough, which increases detection difficulties.

VII. SCOTTISH CENTRES¹.*Scottish fur farms and known escapes from them.*

Thornhill, Dumfries.	Two escaped in 1928, but were said to be accounted for.
Glenbervie, Kincardine.	Two pairs escaped from pens in 1929. October, 1929, one shot near Inverbervie. Said to have bred freely on the Bervie water.
Melrose, Selkirk.	Prior to February 1932, nine were shot in a ditch which connects with the Tweed at Newstead.
Barnton, Midlothian.	—
Huntly, Aberdeenshire.	—
Bishopriggs, near Glasgow.	—
North Kessock, Ross-shire.	A pair was let loose in September 1931, one was killed.
White Moss Loch, Perthshire.	Escapes probable.
Feddal, Perthshire.	Five pairs escaped in 1927, later a male was found dead.



Map 5. Distribution of muskrats in Scotland Oct. 1932—July 1934 from two introduction points: (1) White Moss Loch, and (2) Feddal, Braco.

In connection with the above escapes it may be noted that with the exception of the last one (or possibly two) no further establishment of wild muskrats has been discovered.

In 1927 at Feddal, near Braco, Perthshire, a swamp was made by diverting a stream, and six pairs of muskrats were imported from Canada and turned loose in a wire netting enclosure round the swamp. Five females and four males escaped in the same year. Two years later sixteen lodges were noticed on a marsh on the Ardoch estate near the Allan water 2 miles away from

¹ See also T. M. Munro (1931), *Scottish Nat.* p. 65, and (1934), *Scottish J. Agric.* pp. 94–9.

Feddal. About the same time the embankment of the curling pond at Carsebreck was found to be burrowed into. In 1931 the Allan Water and adjacent marshlands from Kinbuck to Carsebreck were infested, as were also pools on the Orchill estate. These notes on infestation give only a very conservative estimate of the extent of distribution and its spread. This only became known at all accurately when the muskrat campaign was started in October 1932.

In 1929, White Moss Loch, a 15-acre pool near Dunning, Perthshire, was enclosed by wire netting, and four male and eight female muskrats were set free within. The muskrats found the environment very suitable, and bred freely. Though there is no definite evidence that muskrats escaped from this place, there is every likelihood that they did so, as the fence seemed inadequate¹. If this did occur, the infested areas having their centres at Feddal and White Moss Loch have now overlapped.

The area probably became infested as follows. Muskrats from Feddal entered the adjacent Allan Water, and travelled down it to the Forth. This river became infested for a considerable length upstream from the mouth of the Allan. Tributaries of the Forth entering this stretch, notably the Goodie Burn and the River Teith, became infested. The feeders of the River Earn became infested from the headwaters of the Allan, or more probably, infestation was mainly direct from the White Moss Loch centre. The Earn was occupied to its mouth, and stragglers have then gone both upstream and downstream on the Tay, not so far as is now known giving rise to any settled colonies.

The infestation of the waterways is perhaps best described as follows.

River	Length more or less uniformly infested	Distance infested (miles)	Isolated infestations in the river and on tributaries or larger adjacent pools
Allan Water	Kinbuck to Blackford	8	Westerton, Bridge of Allan, Nether Braco, Ardoch Estate, Rhynd Ponds, Carsebreck Ponds, Seathaugh, Orchill, River Knaik, Muckle Burn and hence (?) to Loch Mahaick, Blair Drummond, Upper Lawrick.
Forth	Mouth of Allan Water to Wester Poldar	21	Nether Easter Ofterance, Goodie Burn to Ward of Goodie, Touch Burn.
Teith	Mouth to Mill of Torr	2.5	Callander, Blackwater between Loch Achray and Loch Venacher at Brig-o'-Turk.
Earn	Colquhalzie to mouth	24	Haughs of Pittentian, Pow Water, Pools at Abercairny, Machany Water, Strathallan Castle Pool, Tullibardine, backwaters at South Kinkell, Dalreoch, and Kirkton of Mailer, East Fordun, Gleneagles Golf Course, Broom of Dalreoch, Pool at Sauchie near Aberdalgie, Moncrieffe Pond, Cock Law.

The muskrat in Scotland has spread over a wide area of Perthshire and Stirlingshire. There are several reasons for this. The physical configuration of the country, with two large rivers, the Forth and the Tay, entering the sea not far from one another, and each with a centre of infestation near one of its tributaries. As mentioned above, the results of spread from probably two centres are present. The rivers are generally quite unsuitable habitats for muskrats. The lengths of them mentioned in the table above as infested

¹ The Board of Agriculture for Scotland have since fenced in the Loch so that it is now capable of containing muskrats safely.

have not been as densely infested as is the Severn in Shropshire, and the Arun in Sussex. The Earn, Allan and Teith have but little food growing on their beds, they have few places whose banks are really suitable for burrows, and they are quite rapid and subject to sharp rises and equally sharp falls of water-level. On the land there are few extensive marshes or networks of ditches, such as could support a heavy population of muskrats and would give them little incentive to scatter. The Forth is quite suitable in places both as regards feed and banks to burrow in; the Tay apparently is quite unsuitable, as, so far as is known, none of the many muskrats entering it from the mouth of the River Earn have settled down. When these points are taken into consideration, together with the fact that five years elapsed between the initial escapes in 1927 and the beginning of the trapping campaign, it is not surprising that the population has scattered. It is noteworthy that far more migrant rats wandering from the central area have been obtained in Scotland than in the English infested areas. As in the Shropshire area, weekly catches of muskrats are now low; but trapping is going on over the same area as at the beginning of the campaign, and there are several disquieting instances of old well-established colonies being found privately outside the trapping area which indicate that though the population is by no means as dense as hitherto, its range is increasing. Some of the rivers in which specimens have been sporadically caught (e.g. the Isla) are far more suitable for colonisation than are the waterways of the main area.

Sporadic occurrences of muskrats derived from the infested area.

Date	Sex (if known)	Place	Probable route taken	Approximate no. of miles travelled from nearest centre of infestation
June 10th, 1931	—	Dryburgh, near Dundee, Angus	Mouth of Earn, Firth of Tay, side ditch at Invergowrie	15
May 1931	—	Lindores Loch, Fife	Mouth of Earn, Firth of Tay, stream to loch	5
December 1931	—	Cambusbarron, Stirling	Forth, side ditch	3
May 1932	—	Howietown Fishery, Sauchie, Stirling	Forth, Bannock Burn	15
November 1932	Female	Inchterf, Campsie, Stirling	Firth of Forth, River Carron, River Kelvin	43
April 26th, 1933	Male	Newport, Fife	Mouth of Earn, Firth of Tay	16
May 7th, 1933	Male	Denny, Fife	Firth of Forth, River Carron	31
May 1933	Male	Glamis Castle, Angus	Mouth of Earn, River Tay, River Isla, Dean Water	45
May 1934	Male	Glendoick House, Perth	Mouth of Earn, River Tay, side ditch	4
May 1934	Male	Newbigging, Blair- gowrie, Perth	Mouth of Earn, River Tay, River Isla, Lunan Burn	26
May 1934	Male	Kemback, Cupar, Fife	Mouth of Earn, Firth of Tay, River Eden, Ceres Burn	32
June 1934	—	Harviestoun, Clackmannan	River Forth, River Devon	20



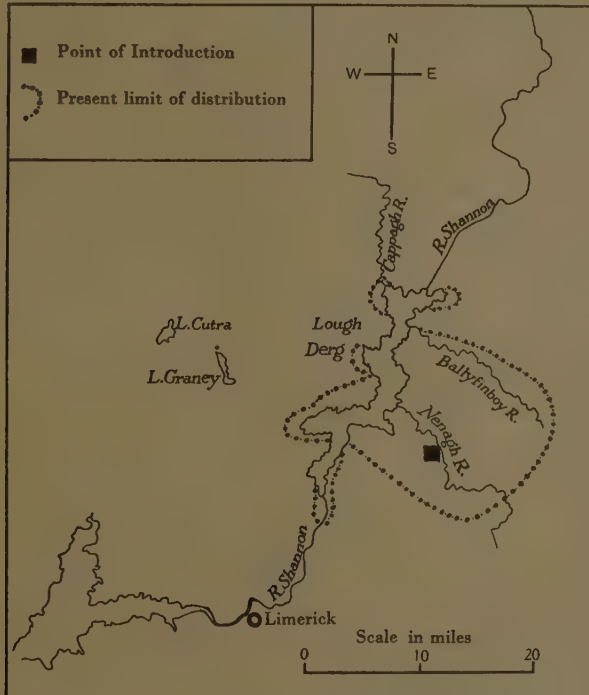
Photo, G. T. Mathhouse

Phot. 3. Muskrat house in Shropshire pond. The separate mouthfuls of vegetation forming the house can be distinctly seen.

VIII. DISTRIBUTION IN IRELAND.

I am indebted for the following details to the Supervisor of the Muskrat Campaign in Ireland.

Musk rats were first introduced into Ireland in July 1927, when a pair were purchased in England and kept at Annabeg, Nenagh, Tipperary. The muskrats are understood to have been originally imported from Malachi, Ontario.



Map 6. Distribution of muskrats in Ireland from the introduction point at Nenagh in 1933-4.

The muskrats escaped after a fortnight in captivity, and nothing further was heard of them until February 1933, when one was shot at Drominies, Nenagh. The Muskrat Campaign was started in September 1933.

An area of approximately 160 square miles is infested and includes all North Tipperary on a line from Killatore-Birdhin east to Roscrea, and from Roscrea north to Portcanna. The district of Mountshannon and Whitegare in East Clare is also infested.

IX. SEASONAL MOVEMENTS.

The periods of increased activity in the muskrat population are shown by sharp rises in catches in spring and autumn. In summer, despite the high percentage of young and more easily trapped animals abroad, the catches fall markedly, owing to the lack of activity of the adults. The females are more inactive than the males during the breeding season, especially immediately after the mating season in March. In spring the population consists almost entirely of adult animals, many of which will be breeding for the first time. The older animals, especially the males, show a well-marked propensity to wander far afield at this time. They seem to lose some of their normal habits during the migration period, and though as a rule they keep to waterways they may, particularly towards the end of their trek, leave these and use roads. The migration urge may carry the males past places suitable for colonisation, in fact, they may and often do travel on to places most unsuitable and until they are emaciated. Most of the animals killed in migration are obtained at the end of April or in May, when they have presumably been travelling at least a month. The females do not wander so far, and tend to settle in places suitable for reproduction. The general bulk of the muskrat population does not wander far, but they are generally active during the spring migration. There seems to be no doubt, from the evidence available, that while the remarkable distances traversed are nearly always made by solitary males, pairs or even a small colony of muskrats may wander far from the infested area.

During the summer months, as has been said, activity is generally at a minimum, but nevertheless there is some movement of single pairs or even of whole families, especially towards the end of the breeding season. In summer local enforced migrations may occur owing to drying up of habitats.

The autumn migration may be connected with the breaking up of the families formed during the summer. Analysis of muskrats caught at this period shows that animals of the first litter are mainly concerned in it, and that both sexes are equally active. While movement within the affected area does undoubtedly take place, there is no extensive movement to new habitats far afield as in the case of the spring migration.

Catches in the open winter of the British Isles do not fall relatively as low as they do in Central Europe, where they approach the low level of summer. In winter, floods may cause movements from the rivers and ditches, but this appears to be less important than is usually supposed.

X. POSSIBLE FUTURE STATUS IN THE BRITISH ISLES.

There are few places in the British Isles which are not capable of supporting a muskrat population. The ramifications of the river and canal systems would provide the animal, if left unmolested, with excellent routes of dispersal from the areas at present tenanted. The muskrat has shown itself very

adaptable to different conditions. In Scotland, failing the presence of suitable slow-flowing water, it has colonised normally fast-flowing trout rivers. Both in Scotland and Sussex tidal waters have been successfully invaded; when migrating, the muskrat is able to traverse many miles of waterways which are unsuitable as a permanent habitat, and to circumvent barriers to a free-water passage. A pair or more may succeed in making such a journey and then will soon found a new outpost.

In the case of a destructive animal such as the muskrat the question of future status largely revolves around the degree of effectiveness of the five control campaigns now being carried out. All the campaigns started work on a more or less large population of animals. At Pulborough and Farnham, where trapping began in March and May 1933 respectively, the heavy initial catches soon slumped. Muskrats have been caught since then, and the last muskrat obtained in either area was trapped at Pulborough in early May 1934. In Ireland the monthly catches have shown a remarkable drop from the beginning, no muskrats having been caught from early May 1933 to date (July 1934). It is known that there are muskrats still at large in all the above three areas. The heavy growth of vegetation in summer and the general inactivity of the adults during the breeding season are two of the causes which diminish the chances of detection and subsequent trapping at this time of the year.

In Shropshire, such was the size and density of the population of muskrats that though a staff of trappers was appointed in June 1932, catches did not show any material reduction until May 1933. This infestation, the largest and densest in the British Isles, has been very materially reduced in area and extent. The Severn is now the only part of the county which is colonised. There is the danger, however, strengthened by the existence of an outpost at Linley for two years, of colonies being established on the Severn many miles below where the present trapping surveillance ends.

The infestation in Scotland is, compared with Shropshire, predominantly one of the pools as distinct from river systems. Muskrats are now being caught in much diminished numbers, though over as great or greater an area than at the beginning of the campaign.

It may be said of all the campaigns that it has not proved a matter of difficulty to reduce materially the density and area of infestation. It is of course impossible to prevent muskrats migrating, and a constant watch on the margins of the infested areas and on places from which muskrats are thought to have been cleared is necessary.

It is likely that many muskrats escaped from musquash farms formerly kept in the country. The holders of licences to keep muskrats during the year ending April 1st, 1933, were obliged to destroy them by that date. A year or two usually elapses between the escape of muskrats and the establishment of colonies dense enough to attract the attention of the public. Sufficient time

has, therefore, not yet elapsed to make sure that other parts of England do not contain infestations. The alternative of relying on the observation of the public is to make a survey of the waterways of England. This is manifestly impossible. The isolated muskrats obtained at the mouth of the Severn near Frampton-on-Severn, Sharpness, and Chepstow point to the existence of a yet undiscovered infestation having its origin at Prestbury, Cheltenham.

It seems that while it is more or less easy to keep the animals well within bounds in the relatively small areas in which they exist in the British Isles, and also to some extent to prevent them from spreading, it is going to be a lengthy and almost impossible task to eradicate them completely. The muskrat will be an expensive member of the British Fauna for several years to come.

APPENDIX I.

MONTHLY CATCHES OF MUSKRATS BY THE CAMPAIGNS OPERATING
IN THE BRITISH ISLES UP TO JULY 1934.

	1932						
	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Shrawardine, Salop	72	243	233	227	201	223	269
(Y not recorded)	—	—	—	—	—	—	—
Farnham, Surrey	—	—	—	—	—	—	—
Pulborough, Sussex	—	—	—	—	—	—	—
Scotland	—	—	—	—	2	27	22
(Y)	—	—	—	—	—	—	—
Nenagh, Ireland	—	—	—	—	—	—	—

	1933											
	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Shrawardine, Salop	104	96	312	112	47	58	54	28	35	35	111	72
(Y)	—	—	—	—	4	18	32	22	28	—	—	—
Farnham, Surrey	—	—	—	—	14	9	6	2	4	1	4	2
Pulborough, Sussex	—	—	22	73	24	6	5	2	—	—	10	2
Scotland	14	27	72	51	51	57	40	78	135	104	62	53
(Y)	—	—	—	—	—	—	—	—	—	—	—	—
Nenagh, Ireland	—	—	—	—	—	—	—	—	59	117	85	36

	1934						
	Jan.	Feb.	Mar.	Apr.	May	June	July
Shrawardine, Salop	11	26	30	20	6	26	21
(Y)	—	—	—	—	—	11	17
Farnham, Surrey	1	1	—	8*	—	—	—
Pulborough, Sussex	4	2	4	4	1	—	—
Scotland	27	19	13	11	17	19	9
(Y)	—	—	—	—	—	6	4
Nenagh, Ireland	19	17	10	12	1	—	—

Totals: Shrawardine, Salop, 2672; Farnham, Surrey, 52; Pulborough, Sussex, 159;
Scotland, 910; Nenagh, Ireland, 356.

Number of young caught in monthly totals is indicated Y=young.

Caught privately before campaign: Shrawardine, 200; Pulborough, 10; Scotland, 140.

(All very conservative estimates.)

* Heavy catch due to discovery of colony in a marsh.

APPENDIX II.

KEY TO MAP OF PLACES WHERE MUSKRATS HAVE BEEN KEPT
IN THE BRITISH ISLES (Map 1).

England.

- Berkshire.*
1. Reading.
2. Hurst.
3. Bracknell.
4. Caversham.
- Buckinghamshire.*
5. Great Missenden.
- Cheshire.*
6. Wilmslow.
7. Runcorn.
- Cornwall.*
8. Illogan.
9. Redruth.
10. Newquay.
- Derbyshire.*
11. Derby.
- Devon.*
12. Honicknowle.
13. Brixham.
14. Torquay.
- Essex.*
15. Rettendon.
16. Colchester.
17. Shoeburyness.
18. Cranham.
19. Newport.
- Gloucestershire.*
20. Prestbury.
- Hampshire and Isle of Wight.*
21. Hambledon.
22. Hamble.
23. Titchfield.
24. Longstock.
- Carnarvon.*
71. Llanwnda.
72. Pwllheli.
- Selkirk.*
78. Melrose.
- Edinburgh.*
79. Barnton.
- Dumfries.*
80. Thornhill.
- Hertford.*
25. Hertford.
26. Cheshunt.
- Kent.*
27. Bexley Heath.
28. Rainham.
29. Maidstone.
30. Dartford.
31. Kingsdown.
32. Edenbridge.
- Lancashire.*
33. Rochdale.
34. Walkden.
35. Freshfield.
36. Caton.
37. Morecombe.
38. Warrington.
39. Silverdale.
- Lincolnshire.*
40. Louth.
41. Grantham.
- Middlesex.*
42. Feltham.
- Monmouth.*
76. Monmouth.
- Norfolk.*
43. Erpingham.
- Northamptonshire.*
44. Northampton.
- Northumberland.*
45. Benton.
- Oxfordshire.*
46. Banbury.
- Shropshire.*
47. Shrawardine.
48. Loton.
49. Middle.
- Suffolk.*
50. Kessingland.
51. Hadleigh.
52. Beccles.
- Surrey.*
53. Farnham.
54. Churt.
55. Egham.
56. Elstead.
57. Tadworth.
- Sussex.*
58. Ticehurst.
59. Eastbourne.
60. Horeham.
61. Pulborough.
- Warwick.*
62. Balsall Common.
- Wiltshire.*
63. Chippenham.
- Worcestershire.*
64. Worcester.
- Yorkshire.*
65. Cottingham.
66. Huddersfield.
67. Helmsley.
68. Shipton.
69. Selby.
70. Leeds.

Wales.

- Glamorgan.*
73. Canton.
74. Pontypridd.

Scotland.

- Kincardine.*
81. Drumlithie.
- Perth.*
82. Feddal.
83. White Moss Loch.
- Ross.*
84. Kessock.

- Montgomery.*
75. Caerwys.

- Aberdeen.*
85. Glass.
- Lanark.*
86. Broomhouse.
- Renfrew.*
87. Neilston.

Ireland.

- Co. Tipperary.*
88. Nenagh.

Isle of Man.

77. Braddam.

NOTES

NOTE ON "A CONTRIBUTION TO TROPICAL AFRICAN BIRD-ECOLOGY."

(J. Anim. Ecol. 3, 41-69.)

DURING my leave in England in 1933 I arranged for certain alterations and additions to this paper as a result of (a) the Editor's decision to hold over a section giving the instrumental records obtained of the Evergreen Forest eco-climate, and (b) additional facts for which I was indebted to the more extensive library facilities in the United Kingdom. Owing to an oversight the amendments were not incorporated in the paper before its publication, although the new references were. I am glad to take the opportunity offered me to explain the appearance of these unconnected references and to make brief mention of one or two of the more important points.

(1) The statement on p. 55 regarding the absence of experimental data on the effect of temperature on birds was to have been modified by reference to Kendeigh's recent work on the Ohio house-wren and the English house-sparrow (*Wilson Bull.* 44, 129, 1932). He found that their behaviour was not disturbed by rising air temperature until 93° F. (=34° C.) was reached, but above that point profoundly. As an indication of which day maxima may have a direct effect on bird distribution this is most important. It may be something more than a coincidence that 35° C. was the temperature at which I observed crows and sparrows in Egypt to show signs of distress.

(2) My statement on p. 52 that between the sun-flecks on the forest floor the light intensity is of the order of one-thousandth of that of the open air was based on about five hundred readings with a Holophane Lumeter.

(3) In support of a hypothesis of the direct effect of humidity on birds one might adduce Rensch's statement (*Proc. 7th Internat. Orn. Cong.* p. 199) that the melanin is increased in a humid warm climate (the so-called Gloger's law) as well as Beebe's claim (*Zoologica*, 1, 1) to have experimentally induced darker plumage in a dove. But as regards the latter the controls are not specified and the experiment does not appear to have been repeated; while natural conditions do not exclude the possibility of a light effect, especially due to the reduction of ultra-violet associated with high humidity.

R. E. MOREAU,

Amani, July 5th, 1934.

A POSSIBLE CASE OF *TREPONEMA CUNICULI* INFECTION IN MAN.

IN 1932¹ I drew attention to the rather common occurrence of syphilitic infections among wild rabbits and hares in various parts of Great Britain, due to *Treponema cuniculi*. In July 1934 I had an opportunity of making further enquiries regarding the occurrence of sores on the hands of men who were

¹ *J. Anim. Ecol.* 1, 84.

in close contact with syphilitic rabbits. The only locality in which I have obtained any evidence of a possible infection from rabbits to man is that of East Harling, Norfolk, between Thetford and Norwich. F. C., a game dealer of East Harling, described an infection of both hands and wrists which he contracted in 1908, at a time when rabbit syphilis was unusually prevalent in that district. The first indication of any infection was the appearance of minute pustules on the skin of the hands; these gradually spread radially until they reached a diameter of about half an inch in the course of three to four weeks. The general appearance and progress of these lesions was stated to be very similar to that of primary syphilides in human beings, but they were all confined to the superficial layers of the skin, not affecting the deeper muscular tissues. About five to six weeks after their first appearance the lesions had healed, leaving red patches on the surface of the skin. Since 1908 no recurrence or new infection has taken place; F. C. is now 71 years old and in very good health. At the same time (1908) several other people in the same district who were in the habit of handling diseased rabbits suffered from the same type of infection, but I could not obtain any certain evidence of its occurrence since that date, although outbreaks among the rabbits have been frequent.

A. D. MIDDLETON.

REVIEWS

THE AUGUST ISSUE OF THE *JOURNAL OF ECOLOGY*
(VOL. XXII, NO. 1).

THE current number of the *Journal of Ecology* contains eight original contributions and a few reviews. Mr Polunin provides the first part of a very full account, illustrated by a great number of excellent photographs, of the vegetation of Akpatok Island in Hudson Strait, for the botanist an entirely virgin field. The data were collected in the "almost incredibly short space of between three and four weeks in August and September 1931. Among the many points of interest which arise the most general is the extreme poverty of the vegetation, which is of markedly "high arctic" character in spite of the comparatively low latitude (60°). The number of species is however considerable. Of the three other descriptions of vegetation Messrs Good and Waugh contribute an interesting account of the flora, dominated entirely by four species of angiosperms, of a transient sandbank in the Humber estuary; Messrs Armstrong, Ingold and Vear publish vegetation and topographical maps of an area of about 48 square miles in the Mourne Mountains (north-east Ireland), in which 12 plant communities are distinguished; and Dr A. S. Watt completes his consideration of the vegetation of the Chiltern Hills with an account of the plateau vegetation, which he compares with that of the corresponding region of the South Downs described in the *Journal* some years ago.

Two papers deal with the chemical relations of plant and soil: Dr Aniela Koslowska provides a careful and thorough study of the effects of plants belonging to different communities on the hydrogen-ion concentration of the medium, in which she obtains some very interesting results; and Mr de Silva, a pupil of Prof. Salisbury, shows reason to believe that the occurrence and vigour of "calcicole" species is more closely correlated with the content of the soil in exchangeable calcium than with the presence of calcium carbonate or with soil reaction. Messrs Chippindale and Milton (Aberystwyth) present a striking study of the viable seeds underlying natural and semi-natural grassland in which a number of unexpected and significant results are disclosed. Prof. John Phillips contributes the first part of an exposition of theories of succession, in which he takes the opportunity of replying to Mr Michelmores's criticisms published in the previous issue of the *Journal*.

The reviews include notices of Schoenichen's book on German forest trees and forest types and Anderson's pamphlet on native British woodlands.

A. G. TANSLEY.

WHITE ANTS.

C. A. Kofoed, S. F. Light, A. C. Horner, M. Randall, W. B. Herms, E. E. Bowe and others. *Termites and Termite Control. A discussion of the biology of termites, and an account of the termites of the United States, Mexico, the Canal Zone, the West Indies, Hawaii, and the Philippine Islands, with recommendations for prevention and control of termite damage by methods of construction and the use of chemically treated and unpalatable woods.* xxv+734 pp., 182 figs. University of California Press, Berkeley, California and Cambridge University Press, London, England, 1934. Price \$5.00 in America, 22s. 6d. in England.

THIS book is a symposium written by thirty-four different authors and is published as a report to the Termite Investigation Committee. As is pointed out in the introduction, its contributions of data, ideas, conclusions and criticisms are in large part the results of

co-operation of men prominent in the large-scale production and utilisation of wood, and scientific men, chiefly members of the faculty of the University of California, interested in specific phases of the subject. Co-operative enterprise of this type merits the highest praise, but unfortunately is all too rare. The volume is divided into four parts of which Part I, Termites and their biology (Chaps. 1-32), contains most of the matter of interest to ecologists, while Part II, Chemical investigations (Chaps. 33-40), Part III, Termite resistivity of wood and building materials (Chaps. 41-45) and Part IV, Prevention and repair of termite damage (Chaps. 46-56) deal with the various economic aspects of the problem. The bibliography at the end of the volume contains less than two hundred entries and there is no index—a serious omission in a work of this size. In the first chapter Kofoid outlines the biological backgrounds of the termite problem and points out their unique place in the natural cycles of water and carbon dioxide, due to their power of breaking up the cellulose of wood. This is followed by a discussion of climatic factors affecting termites, of which the most important are atmospheric and soil moisture and temperature. The fact that some species are able to create and control sufficient moisture in their burrows enables them to live in semi-arid and even in desert regions. Light reviews the constitution and development of the termite colony and points out that, largely as a result of their social habits and the effective protection afforded by closed passageways and chambers, termites have in the course of their evolution become peculiarly lacking in individual protection against either predators or the adverse physical features of their environment. The capture of winged termites by aeroplanes at heights of from 2000 to 3000 ft. leaves no room for doubt that swarming "alates" are at times carried by wind for several miles and is of great significance in the occupation of new territory. Williams' summaries of experimental investigations on factors limiting the distribution of termites barely cover three pages and are much too short considering the importance of the subject. Kirby discusses the association of micro-organisms with termites and concludes that many of the intestinal flagellates are symbiotic, acting upon the wood so that some of its substance is made available for nutrition of the host and receiving in return a favourable environment for their shelter and development. Other non-wood-feeding Protozoa are commensals. The suggestion that the study of these symbiotic Protozoa might aid greatly in showing the true relationships of termites of the *Kalotermes* group reminds one forcibly of V. L. Kellogg's (1913) discussion of the Mallophaga and their hosts. Hendee finds a definite association between termites and fungi, but no evidence of any specific relation between a given species of termite and any genus of fungus. Light lists the following habitat groups: A, Wood-dwelling termites: 1, *Damp-wood termites*; 2, *Dry-wood termites*. B, Earth-dwelling termites: 1, *Subterranean termites*; 2, *Desert termites*; 3, *Mound-building termites*; 4, *Carton-nest-building termites*. The same author discusses the damage done by termites to growing plants. The remaining chapters of Part I deal chiefly with various aspects of the structure, biology, life history and distribution of particular species and groups of species and include useful keys. The book is well planned and well written; apart from the few items mentioned above, and the omission of chapters dealing with the natural enemies of termites and with termitophiles, there seems very little to criticise. Undoubtedly it will stand for a long time as the best "source" for information concerning termites.

B. M. HOBBY.

THE NORTH SEA COD POPULATION.

Michael Graham. *Report on North Sea Cod.* Ministry of Agriculture and Fisheries, Fishery Investigations, Ser. 2, Vol. 13, No. 4, 1-160, 1933. H.M. Stationery Office. Price 7s. net.

The general economic background of this important ecological study is an industry that takes something like a million tons of cod every year out of the seas of the world. The immediate background is an industry, including several nations, that sometimes removes about sixty thousand tons of cod out of the North Sea in one year. In order to study a

more homogeneous part of the cod population, the Norwegian coast of the North Sea is omitted from consideration: from this more limited area some 28,000 tons were landed in England in 1928. It appears that the cod crop in 1927 was worth over a million pounds to Great Britain. Most of the fish are caught now by steam-trawlers, but there is a small subsidiary activity, mostly carried on by line fishing from motor-engined boats, which amounts to about fifteen per cent., and is more important than it looks, since it fills a summer gap in the supplies of cod. Analysis of the British cod-fishery as a whole (first class steam-trawlers for 1928) shows that the North Sea is really an area of comparatively low cod production. It accounted for only 18 per cent. of the total catch, while Iceland fishing grounds provided 63 per cent. But, on account of the greater distance, the fish does not keep so well and it costs more to get there and back; on the other hand the variation of catch per hundred hours fishing varies enormously in different regions, depending mainly on the density of the cod population. The catch per hundred hours at Iceland is twenty times greater than that of the North Sea. The recently developed Bear Island fishery has somewhat changed this picture, and stands now second only to Iceland, and has actually a higher density. In some years (as in 1928) cod heads the list of values, as compared with other species in our fisheries.

These figures give some idea of the importance of knowing as much as possible about the available stocks of cod, the possible dangers of overfishing or underfishing, and the importance of being able to forecast the quality and amounts of the yield from year to year. (The information partly summarised above could have been made more easily available to the reader, if the various units had been standardised; they are rendered variously in hundredweights and in tons and refer to different areas that are rather hard to keep clear in the mind.) The main basis for the ecological study was the statistical material collected by Ministry fishery workers at the ports, supplemented by a certain number of special hauls. As Grimsby does nearly as much cod-fishing as all the other British ports together, and has a wide spread of operations in the North Sea, its figures are taken as being representative. The areas fished are in general similar now to what they were before the War. It is evident that constant effort has been made throughout this work to eliminate both personal bias and sampling errors, or at least to make due allowance for them. Research is hampered throughout by having to obtain its data through the commercial organisation, which is the only one on a scale big enough to produce significant results. Another obstacle to working on cod is that scale readings are not always a safe guide to the age of fish. At the age of three years, as many as one out of four readings are liable to be misleading. Otolith readings are also of little use, at any rate in this area. Most of the analysis therefore depends upon length measurements of samples, and on weights of fish landed. An analysis of very young cod, less than three years old, showed that they had very varying growth-rates according to the region in which they were caught. There is a tendency to fall into two classes, slow and fast growth, and the dividing line between these classes corresponds fairly closely with the colder waters and greater depths in the northern part of the North Sea. The author refrains from trying to explain this correlation of slow growth with colder and deeper water, but shows that it is probably not associated with rough bottom or general density of cod. This line of division had already been shown to exist also in haddock. Most of the Grimsby trawled cod studied come from the fast-growing area for codling.

The frequency curves for size of cod in different months and years are analysed by ingenious methods, which, although they really form the central point of the investigation, cannot be criticised here in detail. Briefly each frequency curve is imitated by a synthetic method which shows the importance of each size-class of cod in building up the whole curve. By the aid of this process it is possible to make hypothetical curves showing the importance of different age-classes. There is no shortage of figures, as 100,000 cod were measured during nine years. Another calculation allows for net selection in affecting the numbers of smaller cod caught. The conclusion is that it is possible by such methods to measure the strength of the young age-classes entering the cod population of marketable size each year. It is also claimed that once the importance of the young brood has been determined, this will be measurable and therefore predictable in future years as the fish

grow larger—in other words that fluctuations from year to year are mainly governed by the size of the young broods. The impression remains that the accuracy of the statistical methods (which are highly technical and ingenious) has outpaced by some distance the reliability of the statistical material. The methods however are in any case of great importance in indicating the type of material which should be aimed at in future. These calculations are however confirmed by a limited amount of reliable work on scales, and also by the general coherence of the results. The numbers from year to year (shown by rough classification of landings by weights) of small, medium and large cod show in general, and sometimes very closely, a correlation with the size of the broods in previous years. This is an important point in confirming the other analyses. We may note in passing the curious quantitative unit of "landing of fish per number of days absence," which in its oddity reminds one of the "flies per boy per hour" of tsetse workers.

The life cycle of cod in the North Sea is discussed and the spawning areas are defined. From these areas (more or less central) the eggs and later the larvae float to their future grounds, on the bottom of which they grow up, eating first Crustacea, and later mainly fish. The closure of the North Sea to fishing for four years during the War resulted in a very great increase in density of the fish, which showed that man has a considerable effect on the age distribution and numbers of the population. The proof that this was not a natural fluctuation lay in the simultaneous increase also of other species such as haddock and plaice, which normally fluctuate independently of the cod. Also it occurred at Iceland and Faroes whose cod variations are not normally correlated with those of the North Sea. In considering this matter, the relations of cod to haddock on which they prey have also to be reckoned. Although theoretically the present stock could again be doubled by protecting specifically the medium-sized cod, there appears to be no means by which this could be done. On the other hand it seems from the evidence that there is no immediate danger of any further overfishing, and the writer of this report believes that the stock is in equilibrium with the fisherman, except in regard to the occurrence of naturally large or small brood years. It is also shown by marking experiments etc. that the North Sea stock is in fact naturally a fairly isolated population which can be treated as one unit for purposes of conservation.

Finally, predictions are made for 1934 and 1935. These are made with great caution, and the results depend to some extent on fishermen maintaining constant methods in future.

The whole report covers a grand sweep of facts and leaves an impression of very energetic team-work concentrated upon a vast mass of material which in turn represents many years' patient collection by a number of workers. The advance in knowledge of the problem during the twenty years since the pre-War period (the results of which were analysed by Russell in 1922) is very striking. Fishery magnates will soon know as much about North Sea cod as any farmer does about his stock, and it is to be hoped that they will have the intelligence to use the information.

CHARLES ELTON.

THE ECOLOGY OF WILD DEER.

M. T. Townsend, M. W. Smith, and C. J. Spiker. *White-tailed deer of the Adirondacks*. Roosevelt Wild Life Bulletins, Vol. 6, No. 2, 1933. New York State College of Forestry at Syracuse University. Price \$1.

THIS bulletin comprises three sections, all dealing with observations on the white-tailed deer (presumably *Odocoileus americanus*) in approximately the same stretch of country. The first two concern the deer in summer, observations being spread over the summers of 1927, 1928 and 1929, and the third is the result of field work in the early spring of 1930 and 1931. Copious use is made of the literature and of information obtained from local residents. There is also an excellent bibliography. It is difficult to understand why the studies made for each section could not have been combined into one more complete survey under the joint authorship of all three observers. As it is, there is a great deal of unnecessary

repetition, especially in the first and second sections, and one has to absorb a great deal of print to obtain a general picture of the life of this animal in its interesting environment.

The Adirondacks form a large area of densely wooded mountainous country (both hardwoods and conifers), with numerous lakes and streams. The real habitat of the white-tailed deer would appear to be the forest-edge zone, which includes open glades, clearings, swamps and the margins of lakes and streams. In the summer months the deer show a marked preference for the margins of lakes, rivers and swamps as feeding grounds, often wading out into the water for algae and other water plants. During the hard winters they are forced to eat practically any vegetation they can get, including leaves, shoots, buds and bark of both hardwoods and conifers, also lichens and roots. During heavy snow there are certain well-defined "yarding grounds" in sheltered spots, where bands of about six to twelve deer feed regularly. There appears to be little doubt that hard winters (heavy snow and temperature continually below zero for periods of several weeks) are the cause of much mortality through starvation-weakness. This and killing by hunters seem to be the principal causes of mortality, as no evidence of disease was obtained. Any critical study of the movements, range and numbers of the deer is made difficult by the large amount of human interference, by "hiking parties" and fishermen in the summer and by hunters in the winter. The white-tailed deer is very shy of human beings in any guise. The evidence available indicates that the range is quite local and that there is no important migratory movement nor emigration. Nothing but vague estimates of the population density were attempted.

In reading this bulletin one feels that the authors must have obtained a great deal more data than they have actually presented. The detailed observations are all scattered in the text as examples in support of various conclusions. One cannot help suggesting that the value of the work would have been far greater to the ecologist if the original field notes had been subjected to careful analytical treatment. Why, for example, could not the observations of deer feeding on different plants have been tabulated and treated statistically by some such means as a frequency polygon? It is far easier to see the relative importance of different observations when some attempt is made at tabulation or statistical analysis of the data.

All three sections are profusely illustrated with photographs, some of which seem rather redundant. There is a tendency in many publications to waste a lot of money on photographs which are often of no use at all in demonstrating a scientific observation. Several useful folding maps of the areas studied during the course of the work are given.

A. D. MIDDLETON.

NOTICES OF PUBLICATIONS ON ANIMAL ECOLOGY

Note. Entomological journals have been abstracted by H. F. Barnes and B. M. Hobby.

Copies of these abstracts, cut down to a width suitable for pasting on to five-inch index cards, are issued free with the *Journal*. They can also be obtained separately by non-subscribers, from the Cambridge University Press, Fetter Lane, E.C. 4, or through a bookseller, price 3s. 6d. per annum post free (about 200 notices, in two sets, May and November).

1. GENERAL PAPERS ON PARTICULAR GROUPS OF ANIMALS.

See also 4 (Tunicata), 61 (Mecoptera), 88 (Echiuridae, Sipunculidae, Priapulidae).

1. Speyer, E. R. (1934). "Some common species of the genus *Thrips* (Thysanoptera)." *Ann. Appl. Biol.* 21, 120-52.

Economic importance of the order and necessity for a revision in the classification are pointed out.

2. Killington, F. J. (1934). "On the identity of *Hemerobius limbatellus* of British authors; with a revised key to the British species of *Hemerobius* (Neur.)." *Trans. Soc. British Ent.* 1, 33-8, 4 pls.

Gives half-tone figures of the wings of all the British species of *Hemerobius* (brown lacewings).

2. ECOLOGICAL SURVEYS AND HABITAT GROUPS.

(a) MARINE.

See also 34, 83, 84, 87, 88, 106.

3. Kitching, J. A., Macan, T. T., Cary Gilson, H. (1934). "Studies in sublittoral ecology. I. A submarine gully in Wembury Bay, South Devon." *J. Mar. Biol. Ass.* 19, 677-706.

The communities of algae and animals down to a depth of 10 ft. below low-water mark were mapped by the use of a diving helmet similar to that devised by William Beebe for tropical surveys. A telephone enabled the observer to give his notes to someone above water. Sample collections were made of selected areas and the dominants mapped, together with associated species. The two main associations were the *Laminaria* (seaweed) "forest" on upward-facing surfaces and the *Distomus* (tunicate)-*Halichondria* (sponge) carpet on vertical or overhanging surfaces. An experiment showed that barnacles (*Balanus*) were important first colonists on bare rock.

4. Thompson, H. (1934). "The Tunicata of the Scottish area: their classification, distribution and ecology. Part IV. Sedentary Tunicata (concluded). Order Krikobranchia." *Fishery Board for Scotland, Sci. Invest.* 1934, No. 1, 1-44.

An excellently produced monograph, with descriptions and illustrations of structure, and also a map for each species showing records of distribution. Information is also given about the habitats.

5. Rogers Brambell, F. W. and Cole, H. A. (1934). "Occurrence of an Enteropneust in Wales." *Nature*, 133, 913.

A species of *Dolichoglossus* found living in sand near low-water mark of spring tides on the coast of Anglesey in Menai Straits. Associated animals are mentioned. Although larval Enteropneusts have often been recorded, adults appear to be rare, this being the fifth record for the British Isles.

6. Renouf, L. P. W. (1934). "Hemiptera inhabiting a salt marsh on the south coast of Co. Cork, I.F.S." *Entomologist*, 67, 129-30.

7. **Brindley, M. D. H. (1934).** "A note on the eggs and breeding habits of *Salda littoralis* L. (Heteroptera, Saldidae)." *Proc. R. Ent. Soc. Lond.* 9, 10.

The eggs of this bug must certainly over-winter in the mud at the edge of the tidal ditches in the marshes, and there must be subjected to all extremes of submersion, desiccation, heat and cold, during their eight or nine months of development. The behaviour of laboratory specimens suggests the possibility that the eggs may be able to exist in a state of suspended development until a second spring comes round.

(b) FRESHWATER.

See also 33.

8. **Balfour-Browne, F. (1934).** "The aquatic Coleoptera of North and South Kerry." *Ent. Mon. Mag.* 70, 28-37.
9. **Pearce, E. J. (1934).** "A contribution towards a list of the aquatic Coleoptera of North Wiltshire." *Ent. Mon. Mag.* 70, 81-7.
10. **Balfour-Browne, F. (1934).** "The aquatic Coleoptera of the county of Angus, with a preliminary list for the county of Kincardine; and with further reference to the *Deronectes depressus-elegans* complex." *Scottish Nat.* 15-25, 41-50.

Contains discussions on the distribution of certain species, without proving any definite conclusions. Gyrinids (whirligig beetles) were unusually scarce in 1933.

(c) LAND.

See also 72, 73.

11. **McWilliam, J. M. (1934).** "The water shrew (*Neomys fodiens*) on Pladda Island." *Scottish Nat.* 99-100.

The water shrew was discovered by a lighthouse-keeper living as a land animal on a small rocky island near Arran, Inner Hebrides. Confirmation was obtained through specimens sent to British Museum. It has now apparently died out through introduction of a cat.

12. **Jary, S. G. and Austin, M. D. (1934).** "Insect and allied pests of cultivated mushrooms." *Ann. Appl. Biol.* 21, 162-71.

Incidence of attacks. Pests associated with buildings or situations, manure or soil and those specific to mushrooms.

13. **Donisthorpe, H. (1934).** "Unusual captures at hawthorn and other blossoms." *Ent. Rec.* 46, 32-3.

Lists representatives of fourteen families of beetles obtained in this way in Windsor Forest. The normal habitat of each species is also indicated.

14. **Newton, H. C. F. (1934).** "On the biology of *Psylliodes hyoscyami* Linn. (Chrysomelidae, Coleoptera), the Henbane flea-beetle, with descriptions of the larval stages." *Ann. Appl. Biol.* 21, 153-61.

Association of *Lonchaea flavidipennis* with the beetle larvae in the damaged stems.

15. **Collin, J. E. (1934).** "Notes on the British species of the genus *Microsania* Zett. Diptera (Platypezidae)." *Proc. R. Ent. Soc. Lond.* 8, 146-7.

"Until 1921 specimens of [the fly] *Microsania* were considered great rarities; but in that year Mons. G. Severin discovered that in various parts of Belgium males could be obtained in hundreds in the immediate vicinity of heath fires, the insects flying even in the smoke and settling on the still hot ground and burnt herbage."

16. **Basden, E. B. (1934).** "*Hydrotaea nidicola* Malloch (Anthomyidae), a new British Dipteron." *Ent. Mon. Mag.* 70, 14-15.

Reared from a rook's nest. Previously known from sparrowhawks' and robins' nests.

17. **Thornley, A. (1934).** "A provisional list of Cornish insects. Part I. Introduction and Hemiptera." Trans. Soc. British Ent. 1, 51-84.

270 species of Heteroptera and 133 Homoptera are recorded from the county. The area considered includes the Scilly Isles.

18. **Davies, W. M. (1934).** "Studies on aphides infesting the potato crop. II. *Aphis* survey: its bearing upon the selection of districts for seed potato production." Ann. Appl. Biol. 21, 283-99.

Includes ecological notes.

19. **Garrett, F. C. (1934).** "The butterflies of Northumberland and Durham." Vasculum, 20, 45-8.

Since the last comprehensive list was published some thirty years ago two butterflies have been discovered and eight have disappeared.

20. **Eastham, L. E. S. (1933).** "Morphological notes on the terrestrial Triclad *Rhynchodemus britannicus* Percival." Proc. Zool. Soc. Lond. 889-96.

This flatworm, already recorded from Yorkshire, Cheshire and Devonshire, was found in Warwickshire and also again in Yorkshire. It was living associated with large numbers of centipedes and carabid beetles; earthworm setae were abundant in the gut. Another species, *R. scharffi*, may occur in England. The differences between the two species are described.

3. ANIMAL BEHAVIOUR AND THE ACTION OF ENVIRONMENTAL FACTORS.

See also 51, 58, 62, 66, 70, 76, 80.

21. **Gray, J. and Ouellet, C. (1933).** "Apparent mitogenetic inactivity of active cells." Proc. Roy. Soc. B, 114, 1-9.

If Gurwitsch is correct in believing that short wave-length radiations are given off by living tissue, it should be possible to detect these by means of physical apparatus. The authors used a Geiger-Müller electron-counter (photo-electric) very similar to that used for detecting faint ultra-violet rays. Fertilised sea-urchin eggs during different phases of mitotic division were used in the experiments. The results were decisively negative, the differences in experiments and controls being insignificant statistically, although cosmic rays produced clear records on the instruments throughout the experiments. This proved that mitogenetic rays, if given off at all, were too weak to have any significance. The same negative results were obtained with growing yeast and active spermatozoa. It was noted that water or other volatile substances (e.g. given off by onions during experimentation) seriously disturbed the counter. The whole forms a serious mass of evidence against the existence of mitogenetic radiation, at any rate on the scale claimed by Gurwitsch.

22. **Renouf, L. P. W. (1934).** "*Zostera* disease on the coast of County Cork, I.F.S." Nature, 133, 912.

Eel grass first began to die off in Cork county in the summer of 1932. By the end of 1933 many beds had completely disappeared, the disease spreading gradually along the south coast of Ireland. Recovery has been rapid in *Z. marina*, *Z. nana*, and in hybrids (all of which were equally affected), except at Castle Haven, where flatfish have decreased too.

23. **Petersen, H. E. (1934).** "Wasting disease in eel grass (*Zostera marina*)." Nature, 134, 143-4.

Further field observations on a fungus associated with dying eel grass in Danish waters. The species of fungus is not yet determined, although spores, etc., have been found. It occurs in a large number of cases where eel grass is dying, and the writer believes it to be the cause of the disease in Denmark.

24. **Gordon, S. (1934).** "The drinking habits of birds." Nature, 133, 436-7.

A discussion which raises interesting problems about the water requirements of wild birds. There are a few field observations as well (gannets, golden eagle, egg stealers such as the hooded crow, etc.).

25. Huxley, J. S. and Howard, E. (1934). "Field studies and physiology." *Nature*, 133, 688-9.

In cold weather the mating sequence of behaviour in male moorhens is slowed down and spread out and may even be stopped. Similar slowing down or inhibition (called "diserotisation") occurs in male rats with part of the preputiary removed, and in dogs which are in a certain mental condition.

26. Edwards, E. E. and Thompson, J. K. (1934). "On the Pigmy Mangold beetle (*Atomaria linearis* Steph.) and methods for its control." *Ann. App. Biol.* 21, 300-18.

Environmental factors affect relative susceptibility of sugar-beet and mangold crops to serious injury by the beetle. Varietal resistance of sugar-beet is noted: mangold as a rule more resistant. New records on garden beet and white goosefoot (*Chenopodium album*).

27. Mellanby, K. (1934). "The influence of starvation on the thermal death-point of insects." *J. Exp. Biol.* 11, 48-53.

High temperature killed starving larval lice *Pediculus humanus corporis* comparatively quickly owing to rapid exhaustion of food supplies caused by the high rate of metabolism and low food reserve. Similar but more marked results were obtained with mosquitoes (*Culex fatigans*) which, when starved, died below their normal thermal death-point.

28. Gunton, H. C. (1934). "Phenological records." *Proc. R. Ent. Soc. Lond.* 9, 1-3.

Outlines a graphical method for scientific recording of phenological results and appeals for volunteers to observe some fifty common species of Lepidoptera.

29. de Worms, C. G. M. (1934). "Early appearances of Lepidoptera, 1933." *Entomologist*, 67, 16.

Further references in E. P. Whitcombe, *ibid.* 17; H. M. Edelsten, *ibid.* 41; S. Morris, *ibid.* 54-6; E. P. Whitcombe, *ibid.* 114.

30. Frohawk, F. W. (1934). "Hibernation of *Vanessa atalanta*." *Entomologist*, 67, 115-16.

Red-admiral hibernating in rabbit burrows. Further reference in N. D. Riley, *ibid.* 138.

31. Nixon, G. E. J. (1934). "Notes on wasps. I. Attempts to domesticate a queen of *Vespa rufa* Linn." *Ent. Mon. Mag.* 70, 37-40.

32. Nixon, G. E. J. (1934). "Notes on wasps. II. On the adoption of an orphaned brood of *Vespa vulgaris* L. by a queen of *Vespa germanica* Fab." *Ent. Mon. Mag.* 70, 87-9.

33. Boycott, A. E. (1934). "Mollusca at Aviemore and the influence of lime." *Scottish Nat.* 1-7.

The molluscan fauna of isolated patches of limestone in this district is much richer than that of the surrounding country. Two species, *Vertigo pinnilla* and *Ena obscura*, had not previously been found so far north. It is suggested that lime enables some species to live in climatic conditions that would otherwise be too severe for them. This was not the case with slugs, which were common both on and off the limestone patches. Notes on freshwater species also given.

34. Ritchie, A. D. (1934). "The habitat of *Procerodes ulvae*." *J. Mar. Biol. Ass.* 19, 663-8.

This marine flatworm (usually called *Gunda ulvae*) lives in the intertidal region where small streams flow down. Pantin had shown that swelling up in fresh water was inhibited by the presence of calcium. The present survey of habitats proves that the worm occurs naturally both in hard and soft water streams. It was found in the latter in the Isle of Man, and in Inverness-shire. In one case there was only 5 mg. of calcium per litre. It can live for five days without sea water, as at neap tides in calm weather.

35. Ellis, W. G. (1933). "Calcium and the resistance of *Nereis* to brackish water." *Nature*, 132, 748.

The polychaete worm *Nereis diversicolor* has a wide tolerance of different salinities. When placed in fresh water it at first swells up and gains weight, and then gets lighter again. Calcium in the water increases its ability to keep out fresh water (as shown by weighing experiments).

36. Spooner, G. M. (1933). "Observations on the reactions of marine plankton to light." *J. Mar. Biol. Ass.* 19, 385-438.

An elaborate experimental study in which copepods, barnacle larvae, other Crustacean larvae, larvae of fish, etc. were used. It is shown that reaction occurs to the direction of light until the animal reaches an intensity of light at which it stays. Migration up to this point is controlled by the direction alone.

37. Poole, H. H. and Atkins, W. R. G. (1933). "Experiments on the suitability of some rectifier photo-electric cells for the measurement of daylight." *Sci. Proc. R. Dublin Soc.* 20, 537-46.

The Bergman selenium cell made by the Weston Electric Company gives approximately accurate results for measurement of daylight, so long as it is carefully tested and calibrated, and its sensitiveness to different parts of the spectrum allowed for.

38. Poole, H. H. and Atkins, W. R. G. (1934). "Some measurements of the brightness of various parts of the sky by means of a rectifier photo-electric cell." *Sci. Proc. R. Dublin Soc.* 21, 1-8.

39. Poole, H. H. and Atkins, W. R. G. (1934). "The use of a selenium rectifier photo-electric cell for submarine photometry." *J. Mar. Biol. Ass.* 19, 727-36.

4. PARASITES OF ANIMALS.

See also 81.

40. Thompson, G. B. (1934). "The parasites of British birds and mammals." *Ent. Mon. Mag.* 70, 133-6.

Association of Hippocidae with bird-lice (*Mallophaga*); and ectoparasites on grey squirrel, badger and long-tailed field mouse.

41. Davis, D. H. S. (1934). "A preliminary survey of the nest fauna of short-tailed voles (*Microtus agrestis* and *M. hirtus*)." *Ent. Mon. Mag.* 70, 96-101.

Includes fleas, ticks, beetles, Collembola, Hymenoptera, flies, Hemiptera-Heteroptera, spiders, Myriapoda and woodlice.

42. Buxton, P. A. (1934). "Separation of lice from hair, wool, or feathers." *Proc. R. Ent. Soc. Lond.* 9, 5.

The material is boiled in a solution of 2 per cent. sodium sulphide and 2 per cent. potassium hydroxide in water until it filters readily. The insects are rendered transparent and difficult to see. They are, therefore, washed off the filter-paper and stained with eosin. When there is much black pigment (which will not pass through a filter-paper), the lice are removed by flotation from liquid paraffin. The methods described have a number of possible applications. They permit one to collect lice with a minimum of trouble from a large sample of material. They should also make it easy to study the changes in seasonal incidence of these insects in populations.

43. Smith, J. (1934). "Sources of infection in undulant fever." *J. Hygiene*, 34, 242-9.

In this country undulant fever is derived almost entirely from cow's milk, the pig and goat types of *Brucella* being apparently absent. Butter and cheese, and direct contact with cattle are negligible as sources of infection. But 17 out of 183 Scottish cows examined had *Brucella abortus* in the milk (9.2 per cent.). In U.S.A. the disease is commonly carried by pigs. Apparently neither horses nor sheep carry it in any country. Fowls are susceptible in the laboratory, but do not normally carry undulant fever.

44. McKenny Hughes, A. W. (1934). "Aphides as vectors of 'breaking' in tulips. II." *Ann. Appl. Biol.* 21, 112-19.

"Self-breaking" selectively transmitted by the aphid vectors *Myzus persicae* and *Macrosiphum gei*. *Anuraphis tulipae* is a vector of "breaking" when attacking the bulbs but not when feeding on the foliage.

45. Jackson, D. (1934). "Parasites of weevils of the genus *Sitona*." *Scottish Nat.* 75-8.

Includes a nematode, a Tachinid fly, Protozoa, and fungi. The fungi caused deaths in Ross-shire to *S. hispidula*, *sulcifrons*, and *flavescens*, and to the last at Wick and Elgin. The infection was transmissible by contact to other weevils and was caused by *Entomophthora coleopterorum*. Another fungus ("the white muscardine") is even more common on *Sitona*. A green fungus ("the green muscardine") also attacks various species, though less commonly.

46. Davies, W. M. (1934). "The sheep blowfly problem in N. Wales." *Ann. Appl. Biol.* 21, 267-82.

Inter alia, complete absence of parasitism among larvae taken from living sheep, greater susceptibility of lambs to attack, and relative susceptibility of attack on six different breeds of sheep.

47. Nixon, G. E. J. (1934). "Two notes on the behaviour of *Volucella pellucens* in its association with the wasps *Vespa vulgaris* Linn. and *Vespa germanica* Fab." *Ent. Mon. Mag.* 70, 17-18.

48. Atkins, D. (1934). "Two parasites of the common cockle *Cardium edule*; a Rhabdocoele *Paravortex cardii* Hallez and a Copepod *Paranthessius rostratus* (Canu)." *J. Mar. Biol. Ass.* 19, 669-76.

High rates of infection with the Rhabdocoele flatworm in various parts of Britain.

5. FOOD AND FOOD-HABITS.

See also 20, 27, 67, 68, 70, 90.

49. Nicholson, C. (1934). "Moths eaten by bats." *Entomologist*, 67, 45.

50. Steven, G. A. (1933). "The food consumed by shags and cormorants around the shores of Cornwall (England)." *J. Mar. Biol. Ass.* 19, 277-92.

Between 1911 and 1915, and again in 1925-9, 10,959 shags and cormorants were killed as a result of bounties offered by the Cornwall Sea Fisheries Committee, which believed them destructive to fisheries, without having, however, made any scientific investigation on the subject. Stomach analyses of 188 shags and 27 cormorants showed that the shags had been eating mainly sand-eels and other non-marketable fishes, such as wrasses, gobies, rocklings, blennies, and dragonets. 37 per cent. had nothing but sand-eels in their stomachs. In the winter months, however, sprats, etc. are also eaten, but the numbers of these fish are too great for shags to have any appreciable effect on them. Only 3 per cent. of shags had eaten flatfish. Of the cormorants, 16 had been feeding in river estuaries, and 14 had been eating flatfish. None had sand-eels in the stomach. The flatfish were mainly flounders, dab and plaice, the total marketable fish forming about 50 per cent. of their food. The cormorant results confirm earlier studies elsewhere, but the harmlessness of the shag to fisheries may be only local. It is thought that there are not more than ten to fifteen thousand shags and one thousand cormorants round Cornwall and Devon.

51. Stonor, C. R. (1934). "Long-tailed duck feeding on sea scorpion." *Scottish Nat.* 50.

One bird had been eating small fish (*Cottus scorpius*) in shallow water—an unusual habit—and died through being choked by the last one it ate.

52. Payn, W. H. (1933). "Kestrel taking bat." *British Birds*, 27, 204.

Remains of a bat, probably a pipistrelle, found in stomach of a kestrel seen hawking for bats at dusk in Suffolk.

53. **Armstrong-Jones, R. (1933).** "Captive cuckoo eating mice." *British Birds*, 27, 203-4.
54. **Halton, H. C. S. (1934).** "Food of yellow hammer." *Scottish Nat.* 29-30.
Young birds fed on moths and caterpillars, mainly Silver Y moths (Dumfriesshire).
55. **Riley, N. D. (1934).** "*Plusia gamma* eaten by yellow-hammer." *Entomologist*, 67, 91.
56. **Thomas, J. F. (1934).** "Species of flies brought by swallows to nestlings." *British Birds*, 27, 231-2.
Flies brought for the young are sometimes disgorged alive and can be collected as they crawl away. Nineteen species (mostly named) belonging to at least nine species were recorded (Carmarthenshire).
57. **Gordon, S. (1933).** "Ptarmigan feeding on scurvy grass." *British Birds*, 27, 210-11.
Seen eating Cochlearia leaves in September on Ben Nevis at about 3800 ft.
58. **Wynne-Edwards, V. C. (1934).** "A lime tree ringed by woodpeckers." *British Birds*, 27, 261-2.
59. **Philips Price, M. (1934).** "Grass-snake preying on young robins." *British Birds*, 27, 230.
Three young robins found in the stomach of a grass-snake.
60. **Wenner, M. V. (1933).** "Vipers preying on young birds." *British Birds*, 27, 176.
"On the moors of North Wales the common viper (*Vipera berus*) habitually preys on chicks of Red Grouse (*Lagopus s. scoticus*) and young Meadow-Pipits (*Anthus pratensis*) and Ring-Ouzels (*Turdus t. torquatus*)." Describes, with photographs, a viper killing a young ring-ouzel, and swallowing a young meadow-pipit.
61. **Hobby, B. M. and Killington, F. J. (1934).** "The feeding habits of British Mecoptera; with a synopsis of the British species." *Trans. Soc. British Ent.* 1, 39-49, 2 pls.
Includes figures of the British species of "scorpion-flies" and drawings of the genitalia. Summarises previous observations on the feeding habits of Panorpidæ and Boreidæ. The new records of the food of *Panorpa* consist entirely of insects which must, in most instances, have been dead, or dead and decaying, when found and eaten by the scorpion-fly.
62. **Spooner, G. M. (1934).** "Observations on *Odynerus (Lionotus) herricki* Sauss. in Dorset." *Ent. Mon. Mag.* 70, 46-54.
Nesting habits, prey, egg and larva of this wasp.
63. **Niblett, M. (1934).** "Some notes on British Trypetidae." *Ent. Rec.* 46, 66-9.
Gives particulars of breeding these flies, names of food-plants and of Braconid parasites.
64. **Gunther, E. R. (1934).** "Observations on the fatty constituents of marine plankton. 1. Biology of the plankton." *J. Exp. Biol.* 11, 173-97.
The volumes of plankton were worked out by a new method, using the relation between volume and length of each species, and then making computations from length measurements of samples. The plankton was from the Isle of Man. The copepod *Calanus finmarchicus* was found to be the most important oil-producing species in the zooplankton. Although these oils appear to be similar to those found in the livers of fish such as the cod and skate, the vitamin A concentration is much higher in fish, indicating some power in the fish of accumulating reserves of vitamin throughout life. They probably get vitamin A mainly from phytoplankton and vitamin D mainly from zooplankton.

65. Collin, G., Drummond, J. C., Hilditch, T. P. and Gunther, E. R. (1934). "Observations on the fatty constituents of marine plankton. 2. General character of the plankton oils." *J. Exp. Biol.* 11, 198-202.

Chemical analyses of the oils.

66. Drummond, J. C. and Gunther, E. R. (1934). "Observations on the fatty constituents of the marine plankton. 3. The vitamin A and vitamin D content of oils derived from plankton." *J. Exp. Biol.* 11, 203-9.

Zooplankton samples from the Isle of Man had hardly any vitamin A in them, but phytoplankton had a good deal (at any rate presence of carotene or related lipochrome pigments was proved). Neither had any strong antirachitic effect on laboratory animals; this showed them to be deficient in vitamin D, the usual condition for phytoplankton but unusual for zooplankton, which may be unable to make vitamin D unless it is irradiated by sunlight near the surface of the sea. These samples were from greater depths.

6. ANIMAL POPULATIONS.

See also 10, 11, 12, 18, 45, 50, 64, 91.

67. Steven, G. A. (1934). "A short investigation into the habits, abundance, and species of seals on the North Cornwall coast." *J. Mar. Biol. Ass.* 19, 489-501.

Seals were accused by fishermen of dispersing mullet shoals and of taking herrings out of the drift nets. Observations showed that seals are pretty numerous, and that they do occur round the herring nets. Identification of seals at sea is very difficult, but grey seals (*Halichoerus grypus*) were definitely seen four times at sea, and also in some numbers near a cave at Boscastle, while three dead ones were found, one of which had herrings in the stomach. One brown seal (*Phoca vitulina*) was seen. Very little is known either about numbers or breeding of these seals. It was advised that destruction should not be undertaken without further investigation.

68. Harrison, T. H. and Lack, D. (1934). "The breeding birds of St Kilda." *Scottish Nat.* 59-60.

A fairly complete census of land birds done on Hirta in 1931. 190 breeding land birds were counted—about one pair to every eight acres. They included 105 rock-pipits, 45 St Kilda wrens, 13 twites, 10 wheatears, and 9 starlings. The rest were raven, hooded crows, meadow-pipits, peregrines, rock dove, and common snipe. Rough counts on Borecray and Soay gave about the same densities, but Dún had one pair to every 2.6 acres: this high density was attributed partly to heavy insect population associated with vegetation near colonies of puffins. The latter are the chief food of the great black-backed gull. Full references are given to St Kilda birds. Past records indicate decrease in hooded crows, starlings, tree sparrows and razorbills.

69. Stewart, M. (1934). "The status of petrels in certain remote Scottish islands." *Scottish Nat.* 95-8.

Visits were made to several islands in the north-west, for comparison with earlier records, of which a list is given. Fulmar petrels have increased on North Rona (none in 1885, 1200 in 1931) and on Sula Sgeir (probably none in 1883, c. 300 in 1932), but not much on the Flannan Islands (a few in 1881, still not many in 1932). Observations were also made on Leach's petrel and the stormy petrel. Notes tendency of fulmars to nest away from cliffs in absence of human interference.

70. Lockley, R. M. (1934). "On the breeding-habits of the puffin: with special reference to its incubation- and fledging-periods." *British Birds*, 27, 214-23.

The puffins visit Skokholm, an island off Pembrokeshire, in thousands in spring and summer. During March and April the birds go 20 to 50 miles out to sea to get food, but spend part of the time on land. In the last 40 years puffins have decreased enormously on Grassholm, but increased on Skokholm, where it is estimated that there are about 40,000 breeding birds, living mainly on the cliff slopes either in rabbit-holes or self-made holes. Shearwaters burrow mainly in the interior of the island, making deeper burrows. The chief enemy of the puffin is the great black-backed gull, which also attacks rabbits and shearwaters. Peregrines also depend mainly on puffins, which

are not normally attacked by lesser-black-backed or herring gulls, by buzzards or carrion crows. Probably the female incubates the eggs, the average period being about 42 days. The young birds are active from birth, and go outside the burrow after several weeks. They are fed on small sand-eels, and on fish-fry which come inshore in June and July. These include herring and pollack. After about 40 days from hatching of the young, the parents desert them. The young migrate by night down to the sea (a photograph of one is given) being thus protected from predatory gulls, etc. They then swim out to sea. This takes place mainly during July and August. They escape enemies by diving.

71. Noble, A. (1934). "Woodpeckers." *Vasculum*, 20, 21-2.

Observes that woodpeckers are spaced about at greater intervals than most birds in woods. They never pack together, and while families of the year keep together till the winter, they separate quickly. Records of Greater Spotted, and Green Woodpeckers from the north of England.

72. Brown, R. L. (1934). "Breeding-habits and numbers of kingfishers in Renfrewshire." *British Birds*, 27, 256-8.

On the 14 miles of the White Cart river studied, there has been increase of kingfishers in recent years. Notes are given on nest-sites, fledging periods, etc.

73. Boyd, A. W. (1934). "Notes on the tree-sparrow, 1933." *British Birds*, 27, 259-60.

At Great Budworth, Cheshire, tree-sparrows had more but not larger broods in 1933 than in previous years. The average number in a brood was 3.61. Among some ringed birds recovered the oldest was four years. Two flies (named) were bred from nests.

74. Ellis, J. C. S. (1933). "Size of swallow broods in Yorkshire." *British Birds*, 27, 202.

The average numbers of young in first broods were 4.88 in 1932 and 4.1 in 1933. This decrease was confirmed by corresponding figures for second broods, which were 4.25 and 4.0 respectively.

75. Thomas, J. F. (1933). "Average broods of swallows in Carmarthenshire." *British Birds*, 27, 201-2.

Gives average numbers of young in a brood for the years 1923 to 1933. The figure for 1933 was lower than any of these years except 1928. The lowest was 3.34 and the highest 4.11 (1931).

76. Boyd, A. W. (1934). "Swallow broods in Cheshire, 1933." *British Birds*, 27, 232.

The average number in a brood, based on the large number of 107 broods, was 4.31. The average per month showed a constant decrease from 4.44 in June to 4.00 in September. The average for the year is higher than that of any of the six previous years and it is suggested that this was due to high temperatures preventing adding of eggs while the parents were away.

77. Ticehurst, H. F. (1934). "Size of swallow broods in Kent." *British Birds*, 27, 232.

Average number in first broods in 1933 was 4.27, in second broods 3.15.

78. Ford, E. (1933). "An account of the herring investigations conducted at Plymouth during the years from 1924 to 1933." *J. Mar. Biol. Ass.* 19, 305-84.

A full discussion of the technique of studying the herring fishery at Plymouth, and the means of developing a forecasting system for the annual yield (including dates, quality and quantity). It is possible to predict the age-composition of the population with some success, but age is not always an index of size. Although ocean current variations may be of great importance in affecting the migration of herring shoals, enough is not yet known to predict these movements at all safely. Changes can be foreshadowed by watching the progress of abundant year-classes of fish in successive years. Results in this direction have been somewhat limited by the fishery statistics available for testing them. Thus factors other than the richness of the available fish population seriously influence the catch taken by fishing vessels.

79. Fryer, J. C. F., Gimingham, C. T. and Buckhurst, A. S. (1933). "Insect pests of crops, 1928-31." Bull. Minist. Agric., Lond., 66, 1-50.

Includes a summary of control methods, notes on foreign introductions, and on incidence of pests classified under different crops. The apple fruit fly (*Rhagoletis pomonella*) reached Liverpool but was detected in time. Further spread of the *Chrysanthemum* midge (*Diarthronomyia hypogaea*) has probably been successfully checked, and it has probably been eradicated, as it occurred primarily under glass. The *Rhododendron* white fly (*Dialeurodes chittendeni*) is firmly established. Cottony cushion scale (*Icerya purchasi*) became established in glasshouses, but was eradicated. Successful control of woolly aphis by the parasite *Aphelinus mali* is claimed for centres at Chislehurst, Kent, and Barnstaple, Devon, but many failures have occurred elsewhere. General notes are given of the annual occurrence of various pests on cereals, potatoë, grass-land, pulse and clover, root-crops and spinach, *Brassica* crops, other vegetables, fruit, tomatoes and cucumbers, bulbs, flowers, hops and willows.

80. Norris, M. J. (1933). "Contributions towards the study of insect fertility. 2. Experiments on the factors influencing fertility in *Ephestia künniella* Z. (Lepidoptera, Phycitidae)." Proc. Zool. Soc. Lond. 903-34.

A very careful statistical study of this flour-moth. The quantity and quality of food supply affects fecundity, but not the viability of the resulting eggs: white flour, instead of wholemeal, reduces fecundity. Light has no effect. At high temperatures infertility increases owing to failure of the males to have successful matings, probably in part due to the retardation of sperm production in the body. Such unsuccessful matings reduce also the number of eggs before laying. At 27° C. 10-59 per cent. of matings were unsuccessful, at 30° C. 96-100 per cent. This effect is emphasised by overcrowding. The average mortality in larvae and pupae at 27° C. was 15 per cent.

81. Salt, G. (1934). "Experimental studies in insect parasitism. 1. Introduction and technique. 2. Superparasitism." Proc. Roy. Soc. B, 114, 450-76.

Experiments on the Chalcidid Hymenopteron *Trichogramma evanescens* and field observations on the Ichneumonid *Collyria calcitrator*, showed that insects tended not to lay eggs in hosts already parasitised, but that their behaviour showed discrimination and was not invariable. "When a number of parasites are distributed among an equal number of hosts, there results neither the 100 per cent. parasitism to be expected from a perfect distribution, nor the 63 per cent. parasitism to be expected from entirely random distribution, but something between them." Mathematical computations of insect population interactions have therefore to take into account the minds of the insects concerned.

82. Johnson, J. R. (1934). "The poplar hawk double brooded during the past season." Vasculum, 20, 32.

83. Russell, F. S. (1933). "The seasonal distribution of macroplankton as shown by catches in the 2-metre Stramin ring-trawl in offshore waters off Plymouth." J. Mar. Biol. Ass. 19, 73-82.

"During the examination of catches it has been noticed that each year has been characterised at some time by the abundance of a species which may occur only in small numbers, if at all, in other years. This has been especially noticeable in the composition of the medusa population." Tables show the abundance of different species on various dates from February 1930 to April 1931. These are intended to form a basis for comparing changes in future years.

84. Jorgensen, O. M. (1933). "On the marine Cladocera from the Northumbrian plankton." J. Mar. Biol. Ass. 19, 177-226.

There are three planktonic water-fleas in the North Sea: *Evadne nordmanni*, *Podon polyphemoides* and *P. intermedius*. This study refers mainly to *Evadne*, which occurs in the inshore waters of the North Sea, breeding twice a year, in spring and autumn, in connection with diatom maxima. Its distribution is much influenced by surface currents, and the writer seeks to explain its variable occurrence in terms of surface currents round the British Isles, and of normal and abnormal hydrographic conditions in different years (four out of ten years are classed as "Exceptional"). This dependence on surface currents is partly brought about by high tolerance to light causing less vertical migration than in some other plankton species. *Evadne* occurs also in the western Atlantic and in the Pacific.

85. Stephen, A. C. (1934). "Scottish records of Cephalopods." *Scottish Nat.* 29.

1933 was apparently a "cuttlefish year," *Eledone cirrosa* and *Loligo Forbesi* being taken in unusual numbers.

86. Moore, H. B. (1934). "The rate of growth of *Balanus*." *Scottish Nat.* 101-9.

A study of age distribution in a barnacle population at Millport (with notes also from the Isle of Man), based on annual growth rings and sizes. *B. balanoides* normally lives about three years, occasionally five, six or more. A colony of *B. balanus* was at least five to nine years old when examined.

87. Stephen, A. C. (1934). "Studies on the Scottish marine fauna: quantitative distribution of the Echinoderms and the natural faunistic divisions of the North Sea." *Trans. Roy. Soc. Edinb.* 57, 777-87.

Detailed maps of the distribution. Abundance of sea-urchins and brittle stars was in general inverse to that of lamellibranch molluscs. The echinoderms were most abundant in the offshore zone. They showed no clear sub-grouping into communities. Petersen's suggested communities for the North Sea do not apply to this group.

88. Stephen, A. C. (1934). "The Echiuridae, Sipunculidae, and Priapulidae of Scottish and adjacent waters." *Proc. R. Phys. Soc. Edinb.* 22, 159-85.

These are all groups which occur rather rarely in collections from the North Sea. Some are really commoner than would appear, on account of burrowing habits; this is shown by their more frequent occurrence in fish stomachs than in collections from the bottom. Details of distribution are given for the North Sea area, based on collections made during the fishery work of the Scottish Fishery Board investigators. There are keys for identification of the species.

89. Kevan, D. K. (1934). "*Spisula (Macra) subtruncata* (da Costa) in the Firth of Forth." *Scottish Nat.* 27.

This species of bivalve, which has in recent years become extinct in the Clyde area and north-west Ireland, still occurs locally in the Firth of Forth.

7. MIGRATION AND DISPERSAL.

See also 36, 70, 73, 78, 79, 84.

90. Monro, T. (1934). "Musk rats in Scotland." *Scot. J. Agric.* 94-8.

A full summary of the introductions, escapes and spread in recent years, with some notes on food habits, migration and the organisation created for muskrat suppression.

91. Beveridge, G. (1934). "The hare in North Uist," 94.

Both mountain and brown hares were introduced in 1890-3. Little was seen of them at first, but in the last ten years they have spread all over the island. Both live together on hill country, and some probable hybrids have occurred.

92. Matheson, C. and Cowley, L. F. (1934). "*Pseudorca crassidens* (Owen) on the Glamorgan coast." *Nature*, 133, 870.

The false killer "whale" (a kind of dolphin) which used to be considered very rare, ran ashore in large numbers in Dornoch Firth in 1927, and has since been reported from South Africa and Ceylon, is probably an inhabitant of open seas. This may account for its rarity in records. In May 1934 twenty-two of these whales were found stranded on the Gower coast of Glamorgan. A photograph of these is given.

93. [Witherby, H. F. and others] (1934). "Recovery of marked birds." *British Birds*, 27, 238-50.

A valuable list arranged under species, giving the place of origin and of arrival in each case. Among other points it is noted that rooks transported as far as 65 miles away from Chipping Norton returned there in some cases. Of 230 rooks taken from there to various other places, nine have been recaptured, and of these five were taken at Chipping Norton.

94. Thomas, J. F. (1933). "Results of ringing and trapping swallows in Carmarthenshire." *British Birds*, 27, 202-3.

Of 96 birds (over a period of four years), only 8 returned to the same shed in the following year and only 2 for two years running.

95. Payn, W. A. (1934). "Migration of robins." *British Birds*, 27, 230-1.

Very large numbers of the Continental race of robin seen on passage along the Norfolk coast at the end of September 1933 (also noted on the coast of Brittany at this time). Such invasions of the east coast do not occur every year, and when they do, apparently penetrate only a short way inland.

96. Richmond, W. K. (1933). "Redlegged partridge in Teesdale, Yorks." *British Birds*, 27, 212.

Not previously known here: had apparently spread and not been introduced.

97. Temperley, G. W. (1934). "The hoopoe in County Durham" and "Nesting of the Quail (*Coturnix c. coturnix*) in County Durham." *Vasculum*, 20, 34.

Both rare occurrences.

98. Groves, W. E. (1933). "Quail in Warwickshire and Worcestershire." *British Birds*, 27, 211.

Bevies reported by three different observers near Stratford on Avon in September 1933, and several birds seen or heard in Worcestershire.

99. Worthington, E. B. (1934). "The changing British fish fauna." *Nature*, 134, 26-7.

A specimen of pike-perch, probably the American *Lucioperca vitrea*, was caught in the River Delph in the Ouse basin in March 1934. It is thought that some eggs of this species were included by mistake in a batch of black bass eggs the young from which were let loose in the Ouse about nine years ago. The pike-perch is a dangerous predator. It is noted also that black bass are established in certain parts of this country.

100. Stephen, A. C. (1934). "Ray's bream in the Firth of Forth." *Scottish Nat.* 27.

One in November 1933. Last big influx to northern waters was in 1927.

101. Delsman, H. C. (1933). "Tunny in the North Sea." *Nature*, 132, 640-1.

1911 is said to have been the first year tunny were noticed by North Sea herring fishermen (but see Russell, Notice No. 87, *J. A. E.*, Vol. 3, No. 1). This year was also remarkable for high temperature of the water, unusually high plankton maxima, and the occurrence of other southern animals besides the tunny (e.g. the tunicate *Doliolum nationalis*).

102. Russell, F. S. (1934). "Tunny investigations made in the North Sea on Col. E. T. Peel's Yacht 'St George,' summer, 1933. Part 1. Biometric data." *J. Mar. Biol. Ass.* 19, 503-19.

Preliminary study of the tunny (*Thunnus thynnus*) which migrate north to British waters in the summer months and are the object of sport of the British Tunny Club. Marked hooks are being used by the Club, so that the movements of fish that get away after being hooked can be followed. A number of fish caught were measured. The region of origin is not at the moment identifiable.

103. Dannreuther, T. (1934). "Migration records." *Entomologist*, 67, 10-14.

Summary of insect migrations in 1933.

104. Wright, A. E. (1934). "Progeny of Immigrant Lepidoptera." *Entomologist*, 67, 92.

105. Donisthorpe, H. (1934). "Marriage (?) flights of some Coleoptera." *Ent. Mon. Mag.* 70, 80.

Contains list of notes by the author on this subject.

106. H[ull], J. E. (1934). "Another phoretic Gamasid." *Vasculum*, 20, 75.

Two nymphs of *Gamasus kempersii* were found attached to a Staphylinid beetle at Belford some three miles from the sea. The adult mites are known to occur associated with rotting seaweed on the neighbouring coast. The author had not previously seen the nymph of *kempersii* attached to any insect, nor any mite at all travelling on a Staphylinid beetle.

107. Orton, J. H. and Rawlinson, R. (1934). "The floating barnacle on the North Cornish coast in the summer of 1933." *Nature*, 133, 418.

Lepas fascicularis occurs normally in the waters of the open ocean in temperate and tropical regions. It is sometimes drifted towards Western Europe in summer. It has been found on the south coasts of England half a dozen times in the last 150 years. The ones found in 1933 were attached to seaweed or floating cinders. A photograph is given.

108. Moore, H. B. (1934). "Occurrence of the floating barnacle in British waters." *Nature*, 133, 651.

Lepas fascicularis found on a floating box off the Isle of Man in April 1933.

109. Russell, F. S. (1934). "On the occurrence of the siphonophores *Muggioea atlantica* Cunningham and *Muggioea kochi* (Will) in the English Channel." *J. Mar. Biol. Ass.* 19, 555-8.

Both species are inhabitants of warmer waters throughout the world. The first occurred every year (except 1915) from 1913 to 1924. The second was first noted in 1925, and came every year (except 1929) until 1931, and again in 1933 and 1934. *M. atlantica* has not been seen since 1924 except once in 1931, when the other was also present.

8. MISCELLANEOUS.

110. Hobby, B. M. (1934). "A bibliography of entomological notes and papers contained in the serial publications issued by local scientific societies in the British Isles. Part II." *Trans. Soc. British Ent.* 1, 85-102.

This, the second instalment, covers the following periodicals: *Rep. R. Cornwall Polyt. Soc.* Vols. 1-77, 1833-1909, and New Series, Vols. 1-6, 1910-30; *Bradford Sci. J.* Vols. 1-3, 1904-12 (all published); *J. Hitchin Nat. Hist. Club*, Nos. 1-12, 1891 (all published); *Proc. Bath Nat. Hist. Fld. Cl.* Vols. 1-10, 1867-1905 (all published); *Proc. Bournemouth Nat. Sci. Soc.* Vols. 1-22, 1908-30; *Proc. Bristol Nat. Soc.* Vol. 1, to Ser. 4, Vol. 7, part 3, 1863-1930; *Trans. Cardiff Nat. Soc.* Vols. 1-63, 1867-1930; *Trans. Watford Nat. Hist. Soc. and Hertfordshire Fld. Cl.* Vols. 1-2, 1875-9 continued as *Trans. Hert. Nat. Hist. Soc. and Fld. Cl.* Vols. 1-18 and Vol. 19, part 1, 1879-1930.

Note. The *Journal of the Society for British Entomology* (formerly known as the "Entomological Society of the South of England"), Vol. 1, part 1, contains notes on breeding records of Hymenoptera and Diptera; the oviposition of *Malachius bipustulatus*; Hymenopterous parasites bred from Hemerobiidae (Neuroptera); oviposition of *Notostira erratica*; Syrphidae (Diptera) associated with flowers; insects at honey-dew; unusual behaviour of *Bombus agrorum*; food of Cantharidae (Coleoptera); Diptera collected in the South of England in 1930-3.

Erratum. Notice No. 30 (vol. 3, No. 1): for "250 c.c." read "litre."

Vol. 3, No. 1

May, 1934

THE JOURNAL
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ANIMAL ECOLOGY

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by
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LONDON
CAMBRIDGE UNIVERSITY PRESS
FETTER LANE, E.C. 4

BOMBAY, CALCUTTA, MADRAS: Macmillan
TOKYO: Maruzen Company Ltd.

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*Annual subscription: thirty shillings (twenty-five shillings
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Price of single numbers: twenty-two shillings and sixpence

THE JOURNAL OF ANIMAL ECOLOGY

Vol. 3, No. 1, 1934 May, 1934

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